

PREDATION BY RESIDENT FISH ON JUVENILE SALMONIDS IN

JOHN DAY RESERVOIR, 1983-1986

Volume I -Final Report of Research

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PREFACE

This document is the final report for two research projects, funded by the Bonneville Power Administration (BPA) Project No. 82-3 conducted by the U.S. Fish and Wildlife Service (FWS) and Project No. 82-12 conducted by the Oregon Department of Fish and Wildlife (ODFW). The Executive Summary summarizes and integrates the results, conclusions, and recommendations of both projects. Section I contains the research papers prepared by FWS and Section II the research papers prepared by ODFW; these papers describe how we addressed project objectives. The papers are listed and numbered consecutively in the Table of Contents and the numbers are used to reference each paper in the Executive Summary. Each paper details conclusions related to its specific objective(s). It is the integration of these individual pieces, however, that can provide the best picture of predation on juvenile salmonids.

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EXECUTIVE SUMMARY

Introduction

Development and operation of the hydropower system in the Columbia River basin has been a major cause of the decline of anadromous salmonids¹. One reason is juvenile salmonids migrating to the ocean suffer high mortality passing dams and swimming through reservoirs. The causes of mortality at the dams were evident and in many cases could be reduced so efforts were focused there. However, causes of and remedies for mortality suffered in reservoirs were not so easily identified and, although evidence existed that suggested reservoir mortality was at least as great as mortality at the dams, little effort was directed at identifying the causes or implementing remedies.

Since development of the Northwest Power Planning Council's (NPPC) Fish and Wildlife Program, reservoir mortality has been identified as an important factor limiting efforts to enhance anadromous salmonids and reach the NPPC goal of doubling the runs. Studies to determine causes of reservoir mortality and ways to reduce it were ranked high by regional managers. Many suspected that predation by resident fish was a major cause of reservoir mortality, especially given changes in the river caused by dams and the introduction into the basin of new predators such as walleye (Stizostedion vitreum), smallmouth bass (Micropterus dolomieu) and channel catfish (Ictalurus punctatus). Along with native northern squawfish (Ptychocheilus oregonensis) these predators pose a real threat to juvenile salmonids which are often concentrated at dams, stressed by the rigors of passing by dams and delayed by reduced current velocities.

In 1982 the NPPC included in its Fish and Wildlife Program measure 404 (c)(1) that called for studies "... to investigate juvenile salmon and steelhead losses to predators while these fish are migrating through Columbia and Snake River reservoirs." In the same year the Bonneville Power Administration (BPA) funded ODFW and FWS to conduct collaborative studies to estimate the number of juvenile salmoids lost to predators in John Day Reservoir. Also included as study objectives were: (1) a description of the importance of predation losses relative to mortality at the dam and total reservoir mortality; (2) a description of how predation losses might vary (spatially and temporally); and (3) recommendations of measures to control predation on smolts.

We studied four species of predator; northern squawfish, walleye,

¹ Northwest Power Planning Council. 1987. Columbia River Basin Fish and Wildlife Program. Portland, Oregon.

smallmouth bass, and channel catfish. Study tasks were:

- 1) Estimate predator abundance and describe their distribution and movements.
- 2) Describe predator growth, mortality, and relative year class strength.
- 3) Estimate rates of gastric evacuation of predators.
- 4) Determine predator food habits, rate of consumption, daily ration, and feeding activity.
- 5) Determine pattern of prey selection by predators as a function of time and reservoir area.
- 6) Integrate data on predator abundance and consumption rates to estimate juvenile salmonid losses to predators.
- 7) Determine the feasibility of reducing predation on juvenile salmonids by various control measures-
- 8) Develop and use conceptual and predictive models to describe the predator-juvenile salmonid relationships in John Day Reservoir.

We selected John Day Reservoir as the study site because the following factors led us to believe if predation was a problem in any reservoir, it would be most obvious there because: (1) the reservoir is an important subyearling chinook rearing area; (2) passage and residualism of juvenile salmonids were considered a problem there; and (3) substantial populations of predators were known to reside in the reservoir.

Northern squawfish, walleye, smallmouth bass, and channel catfish were selected for study as the major potential predators on juvenile salmonids, because previous studies² of resident fishes in John Day Reservoir indicated they were abundant.

We divided the tasks along two lines, one focusing on describing predator feeding habits and one on describing predator populations. The FWS described prey consumption (Tasks 3,4, and 5) and reviewed predator control measures (Task 7) that may be used to reduce mortality of juvenile salmonids resulting from predation. ODFW described the predator populations including estimates of abundance and distribution and a description of predator population dynamics (Tasks 1 and 2). ODFW also integrated the results of both projects; estimating predation losses and mortality (Task 6) and using simulations to describe variation in predation that might result from inherent variation in the system or manipulation through management (Task 8).

2 Hjort, R.C., B.C. Mundy, and P.L. Hulett. 1981. Habitat requirements for resident fishes in the reservoirs of the lower Columbia River. Final Report. U.S. Army Corps of Engineers. Contract No.DACW57-79-C-0067, 180 pp. Portland, OR.

Conclusions

We believe there are several important observations and conclusions that can be drawn from our studies. These include:

1. Predation on juvenile salmonids by northern squawfish, walleye, smallmouth bass and channel catfish can account for a major part, if not all' of the previously unexplained reservoir mortality. We estimated that predators in John Day Reservoir consumed an average of 1.9 to 3.3 million juvenile salmonids annually representing 9% to 19% of the estimated number of juvenile salmonids that entered the reservoir (Paper 8). The losses are of the same magnitude as those estimated for passage through individual reservoirs and 'similar or higher than those estimated for passage at the dam (Paper 8). The estimates are uncertain because of error and inherent variation in components of the estimator but results are most likely conservative (Papers 7 and 8). Predator numbers 'alone could account for the unexplained loss if prey consumption rates approach those commonly reported in the literature (Papers 2 and 7). A significant reduction in predation would result in a significant reduction in mortality of juvenile salmonids in John Day Reservoir.

2. Northern squawfish is the dominant predator on juvenile salmonids in John Day Reservoir. We estimated that northern squawfish accounted for 78% of the total loss to predators observed in John Day Reservoir (Paper 8). Northern squawfish was the only predator that selected juvenile salmonids as the dominant prey during migration peaks (Paper 1) and also aggregated below the dam (Paper 7) where juvenile salmonids were particularly vulnerable. Northern squawfish were more abundant (Paper 7) and had higher juvenile salmonid consumption rates throughout the reservoir than other predators (Paper 2). The relative importance of each predator, however, was not static (Papers 1,2 and 8) and predation activity varied -- e.g. channel catfish were more important early in the migration season and smallmouth bass and walleye were more important later on. Relative importance of each predator can vary depending on levels of recruitment and resulting predator numbers and population structures change (Papers 9 and 10). Walleye, in particular, may become several times more important predators on juvenile salmonid than during our study, but probably will never exceed northern squawfish in total predation (Paper 10). Predator control focusing on northern squawfish should produce the largest changes in reducing juvenile salmonid mortality in John Day Reservoir.

3. Consumption losses of juvenile salmonids by northern squawfish were highest when migration peaked in May and July. Mortality was highest in August. Total ration generally increased with temperature through the season except in June when consumption by northern squawfish declined during their spawning (Paper 2). Mortality, when

age 0 chinook were most abundant, was more than twice that estimated when yearling chinook and steelhead were present (Paper 8). Therefore, increase in juvenile salmonid survival from control of predation should be more pronounced for age 0 chinook than the other stocks. Any estimates of reservoir mortality made over a short period relative to the season or for a single stock of fish can not be considered representative of mortality for all migrants. In general, delays in migration increases mortality of juvenile salmonids because consumption increases when water temperatures increase later in the season (Paper 11).

4. Most predation loss was in the body of the reservoir although the McNary Dam tailrace boat restricted zone (BRZ) had the highest losses per unit area. We estimated 22% of the total loss in the reservoir occurred in the BRZ (Paper 8). Loss was high in the BRZ because consumption rates and density of northern squawfish were significantly higher in the BRZ than elsewhere in the reservoir (Papers 1, 2 and 7). Consumption rates and abundance of other predators 'also varied by location in the reservoir. Consumption rates of channel catfish declined dramatically downriver of the BRZ. Consumption rates of walleye were highest in the mid to lower reservoir (Paper 2), although they were most abundant in the upper reservoir (Paper 7). Consumption rates and abundance of smallmouth bass were high in the lower reservoir (Papers 2 and 7). Control of predation in local areas may be feasible (Paper 5), but may not significantly reduce predation of juvenile salmonids because increased survival in one area of the reservoir may be offset by increased consumption in another area (Paper 11). The magnitude of juvenile salmonid mortality on a reservoir is more dependent on the quality and distribution of predator habitat than the absolute size of the reservoir. Higher than average losses should occur immediately upstream or downstream from dams or in association with complex habitats most suitable for predators.

5. Predation is dynamic and annual variation in total juvenile salmonid consumption and mortality can be substantial. Predation is strongly influenced by abiotic and biotic factors. As temperature increases so do gastric evacuation, maximum ration and general activity of predators (Papers 2,3,4, and 6). Changes in flow affect travel time, relative abundance and vulnerability of prey (Paper 11) and distribution of predators (Papers 7 and 11). Consumption rates can vary as a function of prey composition and abundance (Papers 1 and 6). Predator recruitment and mortality affect losses from predation by changing absolute abundance and relative size structure of predator populations (Papers 7,9,10 and 11). We found that total predation by northern squawfish and walleye may vary at least three fold with the expected natural variation in their populations (Papers 9 and 10). Manipulation of predator recruitment and mortality, juvenile salmonid abundance, and timing of juvenile salmonid passage, could also produce significant changes in mortality (Papers 9 and 11).

6. Direct removal of northern squawfish may be a feasible measure for -reducing predation on juvenilesalmonids in reservoirs. Removal or eradication of predators could produce substantial benefits in juvenile salmonid survival. Limited (10% to 20%) exploitation sustained annually could result in a substantial (> 50%) reduction in predation by northern squawfish (Paper 9); limited exploitation of northern squawfish could be accomplished through a subsidized fishery (Paper 5). Several commonly used measures to remove predators(e.g. chemical piscicides and explosives), are probably not feasible or are socially or environmentally unacceptable (Papers 5 and 8).

7. Reducing encounter rates of juvenile salmonids with predators, by altering project operations, release strategies or bypass structures, may be a feasible measure for reducing their losses to predation. Alteration of project operations, release strategies and bypass structure locations were considered as feasible predation control measures (Paper 5). Re-directing dam lights, using spill to create predator-free zones, or relocating bypass outfalls may be cost effective and viable, even though a relatively small portion (22%) of juvenile salmonid losses to predators may be affected.

8. Consumption rates of juvenile salmonids by northern squawfish can be expected to vary with juvenile salmonid density. The response of northern squawfish consumption rate was not linear or directly proportional to juvenile salmonid density (Papers 6 and 11). Mortality should be most dramatically effected as juvenile salmonid numbers approach very low or very high levels. In both cases mortality should become depensatory, decreasing with further increases in smolt number or increasing as run size declines (Paper 11). Predators can be swamped immediately downstream of the dam at densities of juvenile salmonids observed in recent years. Simulation indicates, however that swamping will not occur within the body of the reservoir until migrants number approximately 120 million. Artificial enhancement (increasing run sizes) or transportation (reduced run sizes) of juvenile salmonids could influence mortality from predation (Papers 6 and 11). Achieving enhancement goals probably will not have a dramatic effect, but transportation in years when runs are low could result in dramatic increases in mortality for juvenile salmonids left to migrate through the system (Paper 11).

Some of our results are uncertain because of important limitations. Many of the limitations are the product of working in a very large and complex system. We have attempted to define the statistical limitations of our data wherever possible. In addition, limitations exist in our knowledge of predation because of the necessarily limited scope of our work (for example we did not study all potential predators, or all months of the year), or the intractable nature of some questions without experimental manipulation. Several limitations are important and useful to consider here:

1. Our present knowledge of juvenile salmonid predation is limited to John Day Reservoir. John Day Reservoir was selected as a site in part, because it is the largest reservoir in the system and could support the highest reservoir mortality. We now believe the magnitude of predation is not necessarily a function of reservoir area, and we don't know how important predation is in other Columbia and Snake river impoundments. Significant reservoir mortality has been documented in the Snake and mid-Columbia rivers and important predators including northern squawfish are present throughout. The physical environment, composition and abundance of juvenile salmonids, and composition and abundance of predators may vary substantially, however. We can surmise that predation is probably an important component of reservoir mortality in other reaches of the river but we can only speculate on its significance relative to other losses or the total mortality.

2. We cannot accurately estimate the proportion of juvenile salmonids consumed by predators that would have died of other causes (e.g. physical injury or disease). Estimates of consumption probably include dead or moribund juvenile salmonids that were injured when passing dams or were diseased. Predators often select weaker or disoriented prey. Sub-lethal stresses from passage, handling at collection facilities or hatcheries, and disease could make many juvenile salmonids more vulnerable to predation. Because we cannot clearly isolate the ultimate causes of mortality the absolute importance of predation is uncertain. Although predation is undoubtedly a major cause of mortality in healthy juvenile salmonids, reductions in predation will not necessarily result in equivalent reductions in total mortality. Elimination of other stresses could result in some reduction of mortality now attributed to predation.

3. Compensation in the northern squawfish population could reduce the benefits anticipated from any removal program. Consumption rates, reproduction and growth could all increase if northern squawfish numbers were reduced (Paper 9). Removals that were not sustained may even aggravate predation by restructuring the population and increasing the number or size of predators. Although we do not believe strong compensation is likely, manipulation of a population will be necessary to understand the response.

4. Interaction among predator fish species in the community could reduce the benefits anticipated from predator control. We could not document the interactions which occur among these predators. In complex natural communities a reduction in abundance of one predator may result in an increase in growth or numbers of other predators. John Day Reservoir supports a community of native and exotic predators that may be very dynamic. We cannot predict the response of that community to manipulation of a single predator population.

5. We do not understand the mechanisms limiting predator recruitment. Temperature and flow may directly influence year class formation of walleye and smallmouth bass (Paper 10). We could not find any physical variable associated with northern squawfish year-class success but walleye could directly control northern squawfish year-class strength through predation (Paper 9). Recruitment of some predators can be affected through reservoir operations (Paper 10). Reservoir management favoring walleye recruitment might actually produce a benefit in juvenile salmonid survival, by limiting the production of northern squawfish. Much better information on recruitment and species interactions is necessary, however, to guide management of resident game fishes with regard to predation.

6. Our results apply to a limited range of environmental conditions. Although we describe some of the inherent variation in predation expected with variation in temperature, flow, and prey composition and number, we derived these relationships from the range of variation experienced during our study (Papers 1,2,6 and 11), from laboratory data (Papers 2,3 and 4) or from other studies (Paper 8). We did not make observations under extremes of flow and temperature. The predator-prey system and resulting mortality of juvenile salmonids may be different under extreme circumstances.

Recommendations

We conclude that predation is a dominant factor in the mortality of juvenile salmon and steelhead in John Day Reservoir. Because of limitations in our data our estimates are uncertain but are probably conservative. If predation causes similar mortality in other reservoirs it is the most important cause of juvenile salmonid mortality. Predation is dynamic and is strongly influenced by abiotic and biotic events. Some of the variation is predictable and some control of predation may be possible by management actions. Further clarification and full consideration of predation is important in future research and management of Columbia River salmon and steelhead. We make the following recommendations for future research and management:

1. New research should describe the relative importance of reservoir mortality and predation throughout the reservoirs of the mid and lower Columbia River and the lower Snake River. Predation may be a less important cause of mortality in reservoirs other than John Day. The development of control or protection measures is not warranted if significant losses occur in only a few reservoirs. A description of the relative importance of predation and total mortality among Columbia River basin reservoirs will help select sites for implementation of control and protection measures. The uncertainty

in absolute predation estimates does not warrant intensive research in each reservoir but rather new work should develop a strategy for "indexing" predation among reservoirs based on short-term surveys.

2. The relative vulnerability of healthy versus dead, moribund, or sublethally stressed juvenile salmonids, to predation should be described. The interaction of predation and other potential mortality and stress is not understood. Additional data collected under controlled conditions could clarify the relative importance of predation and other mortalities.

3. The system planning model(s) should incorporate predation models in the algorithm for reservoir mortality. Salmon and steelhead enhancement will rely on artificial production, flow manipulation, transportation or other management tools that can substantially alter the number, species composition, timing, and travel time of juvenile salmonids. Mortality caused by predation should change as prey number and temporal distribution changes. Modeling can provide an evaluation of the tradeoffs. Models used in our analyses probably cannot be incorporated directly into system models but they can serve as a basis for refinement of the system models.

4. New research should evaluate experimental control of northern squawfish through direct removal. Long term exploitation of northern squawfish could provide substantial benefits in juvenile salmonid survival (Paper 8) but the feasibility of a fishery is unknown. New work should be directed toward gear development, assessment of the social, environmental, and economic ramifications of a subsidized fishery and evaluation of effects of a fishery on northern squawfish populations. If an experimental fishery is initiated the effects of exploitation on population structure and number should be evaluated. Any experimental control should include research describing compensation in the predator population and the community.

5. Research designed to estimate reservoir mortality should account for spatial, seasonal, and annual variability in predation and- presumably the mortality to be measured. Such effort will reduce the error in mortality estimates. New work can test the hypothesis that predation accounts for the majority of reservoir mortality by comparing observed patterns in mortality with those predicted for predation. Experiments that depend on test and control releases of marked fish should try to minimize predation by releasing fish which are not stressed or disoriented and by releasing them away from predator concentrations.

6. The description of the functional response of predator consumption to prey availability should be refined with additional data during the peak migration. The upper asymptote of the response described from existing data (Papers 6 and 11) represents the level of passage where predators become swamped. Some benefit in survival

can be expected with further increases in juvenile salmonid number (Paper 11). Because that point can serve as a critical threshold to enhancement and because the response is poorly defined at high juvenile salmonid densities, better data could be particularly useful to system planning.

7. More detailed research should be conducted on predator recruitment. If an interaction between walleye and northern squawfish exists as suggested here, management of the sport fishery might increase juvenile salmonid survival. Although an approach was not obvious from our results, control of predation may be possible through manipulation of the reservoir.

SECTION I

Introduction

U.S. Fish and Wildlife Service

Project No. 82-3

Contract No. DE-AI79-82BP34796

In 1982 the Bonneville Power Administration (BPA) funded the U.S. Fish and Wildlife Service (FWS) and the Oregon Department of Fish and Wildlife (ODFW) to conduct a collaborative research study to estimate the number of juvenile salmonids lost to predators in John Day Reservoir of the Columbia River. Because of the difficulty and complexity of estimating biological variables in such a large ecosystem as John Day Reservoir, we divided the problem into two broad research areas. The FWS assumed responsibility for the first research area which was to determine the feeding patterns of the major predators in the reservoir. The ODFW assumed responsibility for the second research area which was to describe the abundance and distribution of predators in the reservoir.

The six papers in this section summarize research done by FWS to address the primary study goal-- to estimate smolt losses to predators. To break down the primary goal into manageable components and to provide a fuller understanding of predator-prey relations and the dynamics of predation in John Day Reservoir we developed secondary objectives which were:

- 1) Determine food habits, rate of consumption, daily ration, and feeding activity of major predators inhabiting John Day Reservoir.
- 2) Determine pattern of prey selection of major predators as a function of time and reservoir habitat.
- 3) Estimate the rate of gastric evacuation of major predators inhabiting John Day Reservoir.
- 4) Determine the feasibility of regulating predation on juvenile salmonids by major predators (Joint objective -- FWS lead and ODFW assist).
- 5) Develop conceptual and predictive models of predator-juvenile salmonid relationships in John Day Reservoir (Joint objective -- ODFW lead and FWS assist).

Each of the six papers in this section addresses one or more of these objectives. Paper No. 1 addresses the first two objectives and presents results of the basic food habits analyses and discusses feeding ecology of all four Predators including prey selectivity. Paper No. 2 also addresses the first two objectives and presents estimates of consumption rates and daily rations for all four predators, as well as giving the diel feeding chronology for all predators. Paper Nos. 3 and 4 address objective number 3 and give results of laboratory evacuation experiments on northern squawfish and smallmouth bass and give evacuation rates for both species (gastric evacuation rates did not need to be determined for walleye or channel catfish because their rates of evacuation had already been determined by other researchers). Paper No. 5 addresses objective number 4 and is mainly a literature review of predation control measures and also includes an evaluation of measures plus recommends those most applicable to the Columbia River system. Paper No. 6 addresses objective number 5 and describes an exponential sigmoid functional response model which predicts how northern squawfish consumption rates will vary with changes in smolt density.

The papers in this section represent the majority of final results of FWS research conducted since 1982 when the project was initiated. Additional papers presenting results, supporting documentation, and data appendices may be found in Volume II (see Preface). However, for a more detailed review of the evolution of the project, the sampling designs, intermediate data analyses, and data summaries, we refer readers to the annual reports of progress from this project to BPA (see references Listed below):

Gray, G.A., G.H. Sonnevil, H.C. Hansel, C.W. Huntington, and D.E. Palmer. 1983. Feeding activity, rate of consumption, daily ration and prey selection of major predators in the John Day Pool. Annual Report (1982) to the Bonneville Power Administration. U.S. Fish and Wildlife Service, National Fishery Research Center, Cook, Washington. 81 pp.

Gray, G.A., D.E. Palmer, B.L. Hilton, P.J. Connolly, H.C. Hansel, J.M. Beyer, and G.M. Sonnevil. 1984. Feeding activity, rate of consumption, daily ration and prey selection of major predators in the John Day Pool. Annual Report (1983) to the Bonneville Power Administration. U.S. Fish and Wildlife Service, National Fishery Research Center, Cook, Washington. 65 pp.

- Gray, G.A., D.E. Palmer, B.L. Hilton, P.J. Connolly, H.C. Hansel, and J.M. Beyer. 1986. Section I. Feeding activity, rate of consumption, daily ration and prey selection of major predators in the John Day Reservoir. Annual Report (1984) to the Bonneville Power Administration. U.S. Fish and Wildlife Service, National Fishery Research Center, Cook, Washington. 162 pp.
- Lofy, P.T., S.D. Duke, M.J. Parsley, M.G. Mesa, G.M. Sonnevill, and L.A. Prendergast. 1986. Section II. Predation control measures. Annual Report (1984) to the Bonneville Power Administration. U.S. Fish and Wildlife Service, National Fishery Research Center, Cook, Washington. 162 pp.
- Palmer, D.E., H.C. Hansel, J.M. Beyer, S. Vigg, W.T. Yasutake, P.T. Lofy, S.D. Duke, M.J. Parsley, M.G. Mesa, L.A. Prendergast, R. Burkhardt, C. Burley, D.W. Eib, and T.P. Poe. 1986. Feeding activity, rate of consumption, daily ration and prey selection of major predators in John Day Reservoir. Annual Report (1985) to Bonneville Power Administration. U.S. Fish and Wildlife Service, National Fishery Research Center, Cook, Washington. 105 pp.
- Poe, T.P., D.E. Palmer, H.C. Hansel, S. Vigg, P.T. Lofy, S.D. Duke, M.J. Parsley, L.A. Prendergast, R. Burkhardt, and C. Burley. 1987. Feeding activity, rate of consumption, daily ration and prey selection of major predators in John Day Reservoir. Annual Report (1986) to Bonneville Power Administration. U.S. Fish and Wildlife Service, National Fishery Research Center, Cook, Washington. 50 pp.

Predation by Northern Squawfish, Walleye, Smallmouth Bass, and
Channel Catfish in a Mainstem Columbia River Reservoir:

I. Feeding Ecology During the Salmonid Smolt Out-migration

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ABSTRACT

Diets of northern squawfish (Ptychocheilus oregonensis), smallmouth bass (Micropterus dolomieu), walleye (Stizostedion vitreum vitreum), and channel catfish (Ictalurus punctatus) from John Day Reservoir were examined to determine the extent of predation on juvenile salmonids during their seaward migration (April-August) 1983-1986. Pacific salmon (Oncorhynchus spp.) and steelhead (Salmo gairdneri) juveniles were the most important food group for northern squawfish -- 66.7% by weight, but comprised a lesser gravimetric proportion for other predators: catfish (32.9%), walleye (13.5%), and smallmouth bass (3.7%). Ivlev's electivity index (E_i) indicated that northern squawfish preferred smolts during May and August, generally their peak out-migrations, and switched to prickly sculpins (Cottus asper) when smolt numbers declined. Walleye and smallmouth bass showed preference only for prickly sculpin of all prey fishes tested.

INTRODUCTION

A complex of factors, including human harvest, watershed disruption, and dam building contributed to the decline of the Columbia River salmonid fisheries. Historically, the Columbia River system was the greatest producer of chinook salmon (Oncorhynchus tshawytscha) and steelhead (Salmo gairdneri) in the world (Stone 1878; Evans 1977). Declines of the salmonid runs were not apparent until the boom period of the canning industry in the late 1800's although the runs were still substantial in the early 1930's (Craig and Hacker 1940; NPPC 1984). During 1928-1932, about 3,820 non-native commercial fishermen harvested an average annual catch of approximately 29.8×10^6 pounds (13.5×10^6 kg) from Columbia River stocks, excluding ocean catches; the catch of all salmon and steelhead in 1933 was about 26×10^6 pounds (11.8×10^6 kg) (Craig and Hacker 1940). The Northwest Power Planning Council (NPPC 1986a) adopted a predevelopment salmonid run estimate of $10\text{--}16 \times 10^6$ adults in the Columbia River System; while Chapman (1986) estimated 7.5×10^6 adults, not taking Indian harvest into account. Current total salmonid adult runs are about 2.5×10^6 fish based on dam counts (Chapman 1986).

Overfishing combined with the effects of other poorly controlled activities (e.g., logging, grazing, farming, and mining), plus the construction of dams (for hydropower, flood control and irrigation) caused drastic reductions in Columbia River salmon and steelhead populations (Craig and Hacker 1940; NPPC 1984). From 1933, when the first mainstem dam was completed, to 1975 (completion of the last of 28 dams comprising the Federal Columbia River Power System) the commercial salmon catch declined from about 21×10^6 to 6.6×10^6 pounds (9.5×10^6 to 3.0×10^6 kg) per year. Construction of these dams caused a loss of more than half of the accessible natural spawning habitat (NPPC 1984). Most aspects of the life cycle of anadromous salmonids are affected by hydroelectric development, including blocking upstream migrations of adults, altering the physical environment of the river (e.g., dimension, flow, and temperature), changing the synecology, and increasing the mortality of downstream juvenile migrants via numerous interacting factors (Trefethen 1972; Schwiebert 1977; Raymond 1968). Increased smolt mortality has been caused by such factors as: proliferation of bacterial, fungal, and viral disease from artificial reproduction and rearing; nitrogen gas bubble disease from supersaturation; delayed migrations and asynchronous physiological smoltification; direct mortality from dam turbines; and increased predation (Ebel and Raymond 1976; Ebel 1977; Rosentreter 1977; Raymond 1968, 1969, 1979; Bently and Raymond 1976; Weitkamp and Katz 1980; Zaugg et al. 1985). Predator-prey relationships are fundamental to an understanding of ecosystem dynamics, especially at trophic levels which are directly relevant to fisheries.

The relationships between outmigrating smolts and the predators in the system have been altered due to many of the aforementioned perturbations. The predator avoidance behavior of smolts also has almost

certainly been disrupted by hydroelectric projects causing disorientation during passage, concentration of higher numbers of smolts near projects and the extended migration time for smolts.

Predation has been recognized as an important biological force in structuring freshwater communities (Hrbacek et al. 1961; Brooks and Dodson 1965; Hall et al. 1970; Zaret and Paine 1973; MacLean and Magnuson 1977; Stewart et al. 1981; Carpenter et al. 1985); and the generalization has emerged that top vertebrate predators are dominant (Valiela 1984), e.g. the "keystone predator" concept (Paine 1966). Aside from human harvest, fishes and birds probably effect the greatest predation on salmonids in the Columbia. Ruggerone (1986) estimated that ring-billed gulls (Larus delawarensis) consumed about 2% of the peak spring migration of juvenile salmonids below Wanapum Dam, Columbia River.

The prevalent endemic piscivore in the Columbia River system, northern squawfish, (see Table 1 for list of scientific and common names of all species of fish cited in this paper) has been implicated in causing substantial depletions of juvenile salmonid populations in various waters (Ricker 1941; Thompson 1959; and Jeppson and Platts 1959; Thompson and Tufts 1967). Lake Washington fish communities, which have several species in common with mainstem Columbia River reservoirs, are structured by northern squawfish in a complex way; i.e., predation is significant both on limnetic and benthic-littoral fishes but is mediated by prey switching (Eggers et al. 1978). Northern squawfish primarily feed on the most abundant resident prey species, prickly sculpin, except during seasonal abundances of the predominant planktivore-- sockeye salmon (Eggers et al. 1978). In a review of squawfish predation on salmonids -- with the underlying theme that it was a belief supported by limited data rather than being a scientific fact, Brown and Moyle (1981) concluded that additional studies on squawfish feeding ecology were needed, especially with respect to the effects of dams and to predation during out-migrations of salmonid juveniles.

The numbers of predator species in the system have increased due to introductions of walleye, channel catfish, and smallmouth bass and the endemic northern squawfish populations increasing in response to increased limnetic and littoral habitat. Since these predators are relatively abundant and are known to impact forage fishes in other areas (e.g., Stevens 1959; Wagner 1972; Johnson and Hale 1977; Knight et al. 1984), it has been postulated that they may also impact salmonid juveniles in the Columbia system. In a preliminary study of the effects of walleye feeding on juvenile salmonids and American shad, Maule and Horton (1984) concluded that the impact of predation could not be assessed without fish population estimates.

In response to the forementioned information needs regarding predation, the Bonneville Power Administration (BPA) in 1982 funded studies, conducted jointly by the (United States Fish and Wildlife Service (USFWS) and the Oregon Department of Fish and Wildlife (ODFW), to quantify

Table 1. List of scientific and common names of predator and prey fish species occurring in samples from this study in John Day Reservoir , Columbia River, 1983-1986.

<u>Scientific Name</u>	<u>Common Name</u>
Family: / <u>Genus Species</u>	
<hr/>	
Clupeidae:	
<u>Alosa sapidissima</u>	American shad
Salmonidae:	
<u>Oncorhynchus kisutch</u>	Coho salmon
<u>Oncorhynchus nerka</u>	Sockeye salmon
<u>Oncorhynchus tshawytscha</u>	Chinook salmon
<u>Prosopium williamsoni</u>	Mountain whitefish
<u>Salmo gairdneri</u>	Rainbow trout (Steelhead)
Cyprinidae:	
<u>Acrocheilus alutaceus</u>	Chiselmouth
<u>Carassius auratus</u>	Goldfish
<u>Cyprinus carpio</u>	Carp
<u>Hylocheilus caurinus</u>	Peamouth
<u>Ptychocheilus oregonensis</u>	Northern squawfish
<u>Richardsonius balteatus</u>	Redside shiner
<u>Rhinichthys cataractae</u>	Longnose dace
<u>Rhinichthys osculus</u>	Speckled dace

Table 1. (page 2)

Scientific Name	
Family: / <u>Genus</u> <u>Species</u>	Common Name
-----a-----	
Catostomidae:	
<u>Catostomus</u> <u>columbianus</u>	Bridgelip sucker
<u>Catostomus</u> <u>macrocheilus</u>	Largescale sucker
Ictaluridae:	
<u>Ictalurus</u> <u>nebulosus</u>	Brown bullhead
<u>Ictalurus</u> <u>punctatus</u>	Channel catfish
Percopsidae:	
<u>Percopsis</u> <u>transmontanus</u>	Sand roller
Gasterosteidae:	
<u>Gasterosteus</u> <u>aculeatus</u>	Threespine stickleback
Centrarchidae:	
<u>Lepomis</u> <u>gibbosus</u>	Pumpkinseed
<u>Lepomis</u> <u>macrochirus</u>	Bluegill
<u>Micropterus</u> <u>dolomieu</u>	Smallmouth bass
<u>Micropterus</u> <u>salmoides</u>	Largemouth bass

Table 1. (Page 3)

Scientific Name	Common name
Family: / <u>Genus species</u>	
<u>Pomoxis annularis</u>	White crappie
<u>Pomoxis nigromaculatus</u>	Black crappie
Percidae:	
<u>Perca flavescens</u>	Yellow perch
<u>Stizostedion vitreum vitreum</u>	Walleye
Cottidae:	
<u>Cottus asper</u>	Prickly sculpin

the impact of fish predation on outmigrating juvenile salmonids in John Day Reservoir of the Columbia River. Research on four components of predation was conducted in John Day Reservoir during 1982-1986: (1) feeding ecology, (2) consumption rates on salmonid juveniles, (3) abundance and distribution of predators, and (4) impact of predation on the mortality of out-migrating juvenile salmonids. The major findings of these studies will be reported in a series of four companion papers; this is the first of that series. The purpose of this paper is to document the feeding ecology of the potentially important predators of salmonid juveniles in John Day Reservoir --- northern squawfish, walleye, smallmouth bass, and channel catfish. The specific objectives of this study were to: (1) quantify the diets of these four fish predators, (2) compare their diets on a temporal and spatial basis, and (3) evaluate the dynamics of their diets with respect to the juvenile salmonid out-migration.

STUDY AREA

The study took place in John Day Reservoir in the Columbia River; the longest river in North America (1,950 km), with the second greatest flow rate in the [United States (average of $5.7 \times 10^3 \text{ m}^3/\text{s}$ and one of the most altered (Trefethen 1972). Its drainage basin consists of $6.71 \times 10^5 \text{ km}^2$, including: most of Washington, Oregon, and Idaho; parts of Nevada, Utah, Wyoming, and Montana; and $1.0 \times 10^5 \text{ km}^2$ in British Columbia where it's headwaters begin in the Canadian Rocky Mountains (Figure 1). From upstream, the principal tributaries of the Columbia are the Kootenai, Pend Oreille, Okanagan, Wenatchee, Yakima, Snake, Willamette, and Cowlitz rivers. The Columbia forms an estuary before discharging into the Pacific Ocean, and the lower 234 km has tidal influence. Hydroelectric development has been the major factor in alteration of the Columbia River system. Rock Island was the first (1933) mainstem dam on the river, followed by Bonneville Dam (1938) which was the first federal project and is lowermost in the system. In 1941 the second federal project, Grand Coulee Dam, was completed and effectively blocked all salmonid migrations into the Upper Columbia River. An additional fourteen major dams have since been constructed on the Columbia and Snake rivers.

John Day Dam was built in 1968 at river km 347, is the third dam upstream from the ocean, and forms the longest reservoir (123 km) in the lower Columbia River -- extending to McNary Dam (the "lower Columbia River" can be defined as that stretch downstream from McNary Dam). John Day Reservoir has a mean elevation of 89 m above mean sea level, a mean width of 1.8 km, a mean depth of 8.0 m, a maximum depth of 44.2 m, a surface area of about 21.34×10^9 hectares, and a capacity of about $1.69 \times 10^{15} \text{ m}^3$ (?). Peak discharges of about $64 \times 10^3 \text{ m}^3/\text{s}$ from McNary Dam generally occur in April and minimum flows occur in November. Water residence times vary directly with flow, since there is little storage capacity.

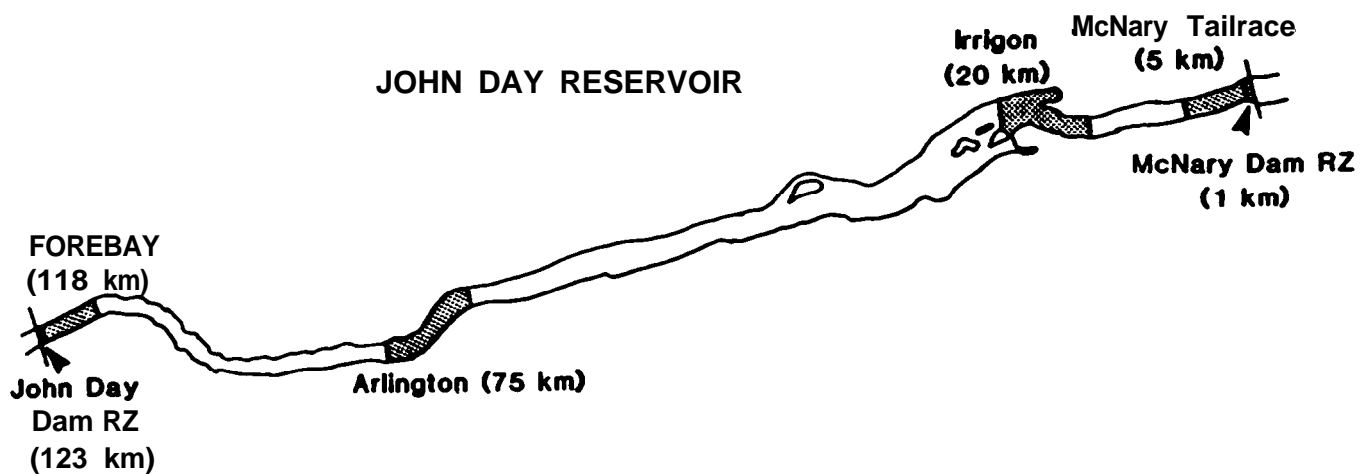
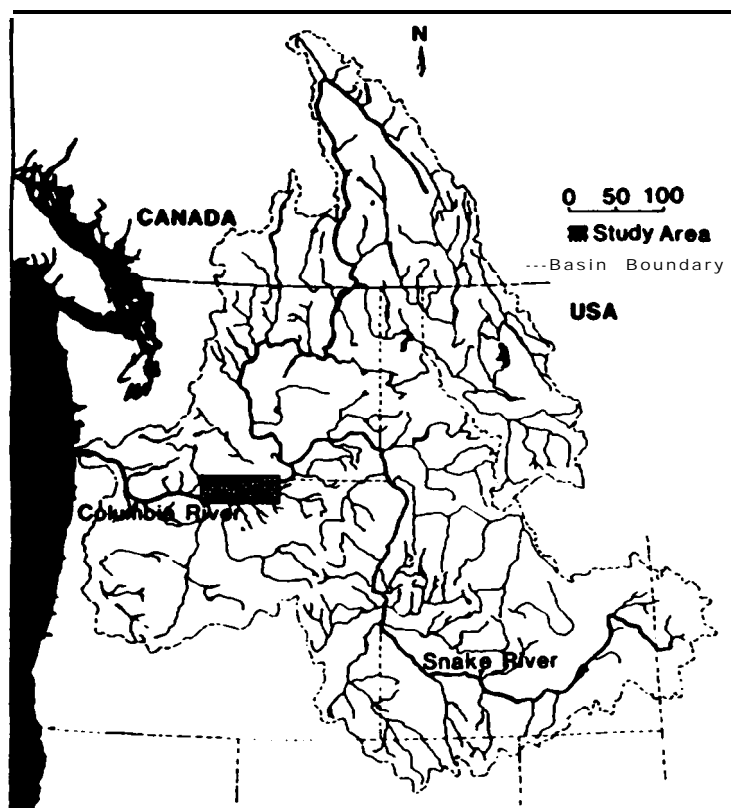


Figure 1. Location of sampling stations (shaded areas) in John Day Reservoir and the study area in the Columbia River Basin.

Temperature ranges from 0 to 27°C with minima generally occurring in February and maxima in August. Thermal layering occurs during summer, however it is intermittent temporally and incomplete on spatial basis -- and the reservoir may therefore be considered polymictic. On the basis of nutrients and primary production, John Day Reservoir may be categorized as mesotrophic (Hjort et al. 1981).

SMOLT OUT-MIGRATION

The fish community of John Day Reservoir is comprised of an assemblage of 34 species -- representing both resident and anadromous life histories (USFWS unpublished data). The spawning migration of adult anadromous salmonids passing John Day Dam and entering the reservoir during 1983-1986 was comprised of 50% chinook, 27% steelhead, 20% sockeye, and 4% coho; these proportions have been similar since the dam was closed in 1968 (U.S. Army Corps of Engineers 1986).

Hatchery production of anadromous salmonids upstream from McNary Dam (Mid-Columbia and Snake rivers) during 1983-1986 averaged about 35 million fish per year, with the following overall percent species composition: fall chinook, 38.5; spring chinook, 33.1; summer chinook, 6.4; coho, 1.4; and steelhead, 20.6 (Fish Passage Center 1986). The spring chinook, coho, sockeye, and steelhead generally out-migrate as yearlings, whereas the summer and fall chinook out-migrate as sub-yearlings. Natural reproduction, primarily in the free-flowing Hanford Reach, is relatively high for fall chinook. The Passage Index (dam counts adjusted by flow) of juvenile salmonid emigrants at McNary Dam estimated the following relative abundance: 34.6% chinook yearlings, 40.8% chinook sub-yearlings, 1.7% coho, 10.3% sockeye, and 12.6% steelhead (Fish Passage Center 1986). Smolt emigration occurs from April through August; the majority of chinook sub-yearlings migrate during July, while the peak migrations of the other groups occur in May (Figure 2).

METHODS

Sampling Field Procedures

Diets of predators were monitored from 1983 through 1986 by sampling five locations in John Day Reservoir (Figure 1 and Table 2). The McNary Dam tailrace (river km 463-470) and boat restricted zone (river km 470-470.5) stations represented areas influenced by turbine outflow and spill. Irrigon (km 444-458) was a transitional zone but mostly was similar to the tailrace area. The mid-reservoir station, Arlington (river km 387-399), typified reservoir habitats away from the direct influence of dams. The John Day forebay station (river km 347-354) represented an area where juvenile salmonids may concentrate prior to dam passage. All sampling stations were established in 1983 except Arlington

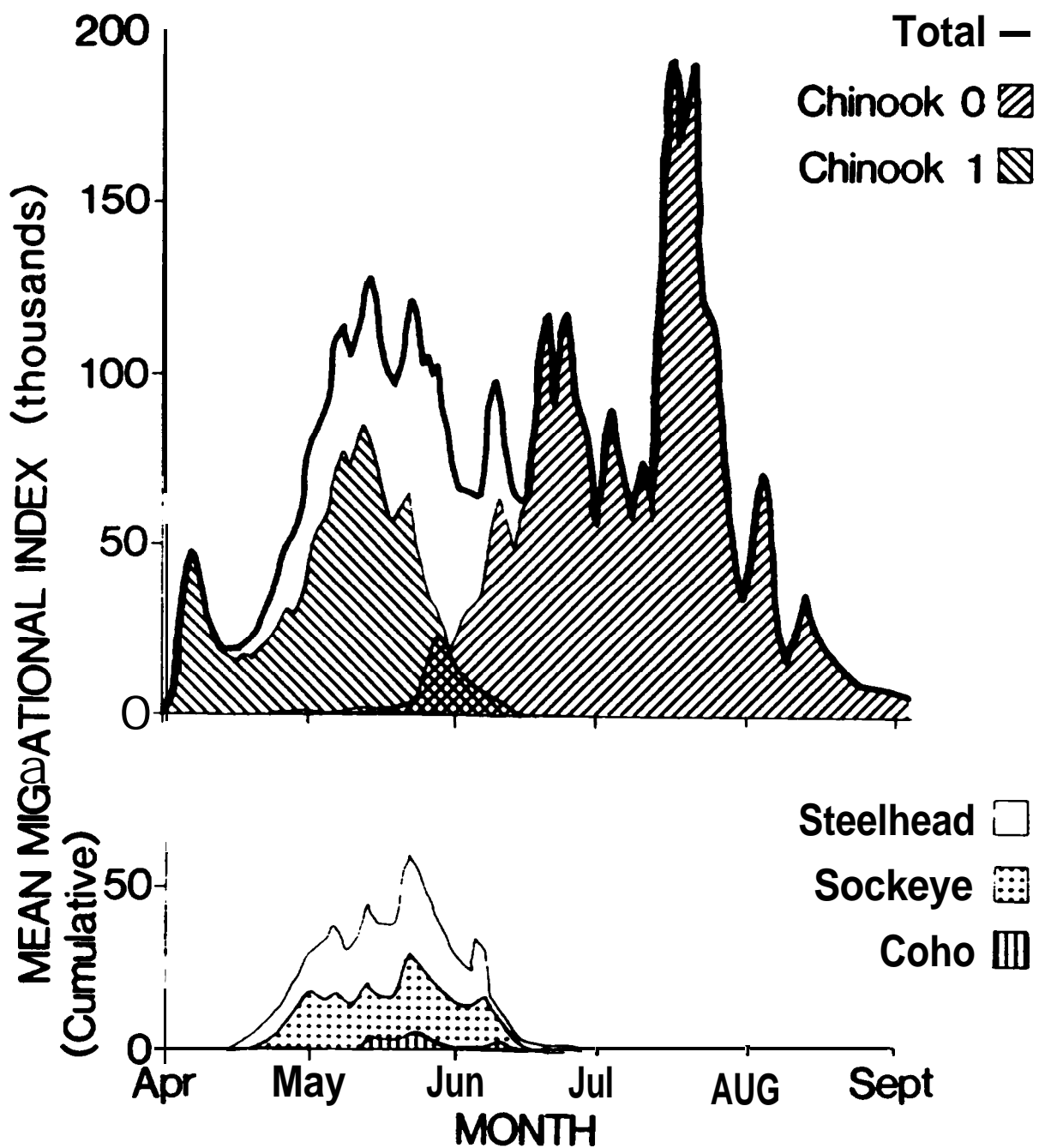


Fig. 2. Timing and relative abundance of the smolt downstream-migration through McNary Dam, Columbia River, 1983-1986.

Table 2. Sampling design in John Day Reservoir, 1983-1986.

Year/Month	Station				
	McNary	McNary BRZ	Irrigon	Arlington	Forebay
<u>1983</u>					
April	+ ^{1/}	+	+	0	+
May	+	+	+	0	+
June	+	+	+	0	+
July	0	0	0	0	0
August	+	+	+	0	+
<u>1984</u>					
April	+	+	+	+	+
May	+	+	+	+	+
June	+	+	+	+	+
July	0	0	0	0	0
August	+	+	+	+	+
<u>1985</u>					
April	+	+	+	+	+
May	+	+	+	+	+
June	+	+	+	+	+
July	+	+	0	0	+
August	+	+	+	+	+
<u>1986</u>					
April	+	+	0	0	0
May	+	+	0	0	0
June	+	+	0	0	0
July	+	+	+	+	+
August	+	+	0	0	0

^{1/} + = samples collected.

0 = no samples collected.

which was established in 1984.

Predators were sampled monthly at each station on a diel schedule (with four consecutive six-hour periods each day for a minimum of three consecutive days) from April through August each year, however, no July samples were collected during 1983 and 1984. During 1986, the boat restricted zone station was sampled biweekly from April through August; all other stations were sampled only during July. Although the sampling design was not consistent and balanced within or among years (Table 2), all combinations of locations and months were covered adequately over the four years. Because of this broad coverage and the fact that spatial and temporal food habits data were generally consistent from one year to the next (e.g. consumption of yearling chinook salmon by northern squawfish was highest in May at McNary tailrace for all four years), we pooled data or used averages across months, years, or stations to increase sample sizes without sacrificing accuracy. Predators were collected primarily with a boat electroshocker. However, a 9 m (headrope) semi-balloon bottom trawl, and multifilament gill nets measuring 60 by 1.8 m with 8.9, 10.2, 12.7, or 15.2 cm stretch mesh were used to collect walleye and channel catfish.

Food Habits Procedures

Predators were anesthetized with benzocaine, weighed to the nearest gram, and their fork lengths (FL) measured to the nearest millimeter. Stomachs of smallmouth bass greater than 100 mm in length and walleye greater than 200 mm in length were pumped using a modified Seaburg (1957) sampler to obtain stomach contents. Entire digestive tracts were removed from channel catfish and northern squawfish greater than 250 mm in length. Smallmouth bass less than 100 mm, walleye less than 200 mm, and northern squawfish less than 250 mm in length were preserved whole. All collections were preserved immediately with 10% formalin.

Stomach contents were identified to the lowest practical taxon and enumerated under a dissecting microscope. Individual prey items were blotted dry and weighed to the nearest milligram. Typically, crustaceans were identified to genus or family and insects to family or order. Fish were identified to species or genus and measured (fork length) to the nearest millimeter. Partly digested fishes often were identified by their bone morphology, as determined from a reference collection (Hansel et al., In Press). When fork length could not be measured directly because of digestion it was estimated from standard or nape to tail lengths or bone lengths (Hansel et al., In Press) using regression equations developed from known specimens. Partially digested fish remains from more than one prey fish were weighed together and apportioned to the weight of individual prey fish based on the relative weight of individual prey fish and their degree of digestion. When only digested fish parts remained and the relative size of each prey fish could not be determined,

the total weight of the parts were divided equally among fish in the stomach. Parasites, non-food items, and unidentified material were noted during examination, but excluded from dietary calculations.

Prey Species Selection

To determine if predators preferentially selected certain species of prey fish disproportionate to their availability in the reservoir, we collected prey availability data by beach seining (Parsley et al. In Press) in 1984 and 1985 in the same locations/habitats where predators were sampled. For prey selectivity analysis, John Day Reservoir was divided into upper (McNary Dam tailrace and Irrigon), middle (Arlington), and lower (John Day forebay) sections. The only habitat in the reservoir not represented with availability data was the boat restricted zone (BRZ). In the BRZ, dam passage information on juvenile salmonids (Fish Passage Center 1986) was used to determine the availability of prey fish and was applied solely to northern squawfish, the only abundant predator present (Beamsderfer et al., 1988).

Predator preferences for various prey fish species were determined using Ivlev's (1961) electivity index (E_i). This index was selected because it has been the most frequently used electivity index and there is no wide consensus on which index to use (Lechowicz 1982). Because ingested prey could not always be identified to species, prey ingested and prey available were lumped into prey groups at genus or family level. Index data were pooled for 1984 and 1985 to increase the sample sizes and because there was little variation in electivities between years.

Prey Size Selection

To determine if northern squawfish were feeding selectively on certain sizes of juvenile salmonids at McNary Dam BRZ, we compared the length distributions of salmonids in the stomach contents to lengths of those sampled from the environment (Washington Department of Game - unpublished data). Lengths of juvenile salmonids were pooled for all years by month because length distributions did not vary among years. To estimate relative abundance of vulnerable prey we used linear regression to relate maximum length of ingested prey to predator length. The largest ingested individual of each prey type was regressed against the length of the predator, stratified by 25 mm intervals. Salmonid prey length frequency distributions, by 10 mm length intervals were compared in the stomach contents versus environmental samples and Ivlev's E_i was calculated.

Data were entered into an IBM AT micro-computer for analysis. Mean number, percent composition by number, percent composition by weight, and percent occurrence were calculated. These indices were used to analyze relationships between diet and capture location, time of capture, size, and season for each predator species.

RESULTS

General Diet

Fish was the dominant prey group (by weight) for all four major predator species in John Day Reservoir (Table 3). Only for northern squawfish, however, were juvenile salmonids a dominant (by weight) prey item (Table 3). Salmonids also were the prey fish most frequently consumed by northern squawfish (33.5%), while about 20% of all walleye and channel catfish consumed salmonids, and only 2.8% of all smallmouth bass consumed salmonids. On an overall frequency of occurrence basis, fish, crustaceans, and insects occurred in roughly the same proportions for northern squawfish, smallmouth bass, and channel catfish, but walleye were almost totally dependent on fish (96.4%). Next to fish, crayfish (Decapoda) were the second most important food item (by weight) for northern squawfish, smallmouth bass and channel catfish. Insects were frequently consumed by the predators but comprised very little of the bulk in their diet.

Northern Squawfish - Of the 4783 northern squawfish collected (30-586 mm FL), 69% had food in their digestive tracts; 51 taxa of prey were consumed, comprising six major groups (Table 3). Frequency of occurrence and relative proportions by weight of salmonids and other food items in the stomach contents of northern squawfish were consistent over years and therefore were pooled for 1983 - 1986, but differences did occur among areas within the reservoir (Figure 3). Salmonids were of greatest importance in the diet of northern squawfish near the dams at McNary Dam tailrace and John Day Dam forebay where they accounted for 78 and 66% of the diet, respectively. In contrast, salmonids comprised only 8 and 19% of the diet at Irrigon and Arlington. The most important prey in those areas were cottids which comprised 52% of the diet at Irrigon and crayfish which comprised 40% of the diet at Arlington.

The importance of salmonids in the diet of northern squawfish also varied seasonally (Figure 4). During April through August, salmonids ranged from 44 to 81% (by weight) of the diet. Salmonids as a group accounted for 68 and 73% of the food items eaten during April and May when the yearling chinook, sockeye, and coho salmon and steelhead trout emigrations were peaking. Steelhead were most important in the diet of northern squawfish in May when they represented 23% of the diet. Salmonids were of less importance in June (46%) as the yearling salmonid emigration (Figure 2) neared an end and squawfish switched to crayfish (22%) and prickly sculpins (15%). Salmonids were of greatest importance in the diet during July (82%) when the run of subyearling chinook salmon (Figure 4) peaked. In August, with the decline in numbers of emigrating subyearling chinook, the contribution of salmonids to the food items was

Table 3. Percent frequency of occurrence (% FO) and percent by weight (% WT) of all prey groups consumed by northern squawfish (NSQ), walleye (WAL), smallmouth bass (SMB), and channel catfish (CHC) in John Day Reservoir (all stations and months combined) 1983-1986.

PREY GROUP	NSQ		WAL		SMB		CHC	
	% FO	% WT	% FO	% WT	% FO	% WT	% FO	% WT
Fish (total)	47.0	80.9	96.4	99.7	60.7	77.6	48.8	68.3
Petromyzontidae	1.1	0.2	0.0	0.0	0.0	0.0	0.1	0.0
Salmonidae (total)	33.5	66.7	20.7	13.5	4.0	4.2	18.9	32.9
Salmon spp.	27.8	48.2	10.8	8.3	1.5	2.5	6.5	13.6
Steelhead	3.5	13.5	0.9	2.3	0.0	0.0	1.3	4.5
Salmonidae (unid.)	4.4	5.0	12.3	2.7	2.5	1.7	13.7	14.6
Catostomidae	1.1	1.7	27.5	40.1	12.3	22.6	1.7	3.2
Centrarchidae	0.1	0.0	0.0	0.0	1.1	0.5	0.1	0.1
Clupeidae	1.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Cottidae	6.7	7.3	22.0	15.9	27.4	32.5	15.5	19.4
Cyprinidae	0.8	1.4	12.4	11.3	6.8	11.6	3.1	5.2
Ictaluridae	0.0	0.0	0.3	0.1	0.1	0.1	0.1	0.0
Percopsidae	3.6	2.4	27.3	16.7	6.3	5.0	2.3	0.5
Unid. non-salmon	0.5	0.2	21.6	1.9	10.8	1.0	10.9	4.2
Crustacea (total)	48.3	13.4	8.6	0.0	60.3	21.3	65.3	18.4
Cladocera	0.2	0.0	0.0	0.0	5.0	0.0	0.0	0.0
Copepoda	0.0	0.0	0.1	0.0	2.1	0.0	0.1	0.0

(Table 3. continued)

Prey Group	NSQ		WAL		SMB		C CAT	
	% FO	% WT	% FO	% WT	% FO	% WT	% FO	% WT
Amphipoda	35.5	3.4	8.3	0.0	34.0	0.5	42.4	0.2
Isopoda	0.1	0.0	0.0	0.0	0.2	0.0	0.3	0.0
Decapoda	17.1	9.9	0.1	0.0	33.6	20.7	31.0	18.1
Insecta (total)	43.8	2.3	11.8	0.0	36.8	0.6	34.4	0.9
Diptera	13.3	0.1	3.5	0.0	19.8	0.1	10.5	0.2
Ephemeroptera	22.1	0.6	6.4	0.0	12.4	0.3	21.9	0.5
Hemiptera	2.0	0.0	0.1	0.0	1.1	0.0	0.1	0.0
Homoptera	2.4	0.0	0.5	0.0	1.1	0.0	0.3	0.0
Hymenoptera	7.1	0.3	0.0	0.0	3.2	0.1	1.7	0.0
Coleoptera	7.0	0.1	0.9	0.0	1.5	0.0	1.7	0.0
Trichoptera	1.0	0.0	0.9	0.0	1.7	0.0	1.5	0.0
Unid. insects	15.6	0.9	1.6	0.0	5.4	0.1	2.3	0.2
Mollusca (total)	3.8	0.6	0.7	0.0	0.7	0.0	9.7	5.2
All Other Food	15.9	2.6	9.0	0.1	13.1	0.1	29.2	7.0

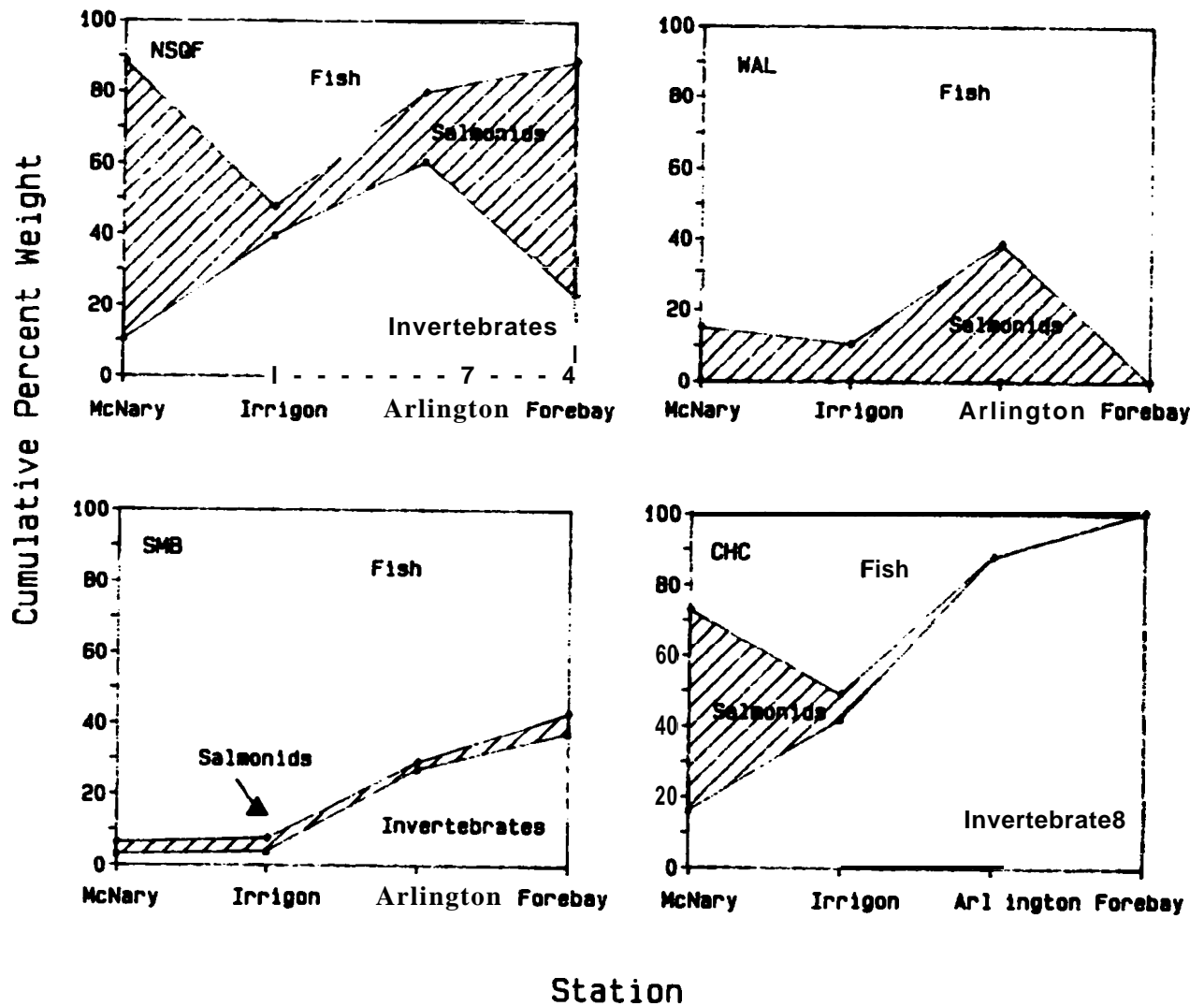


Figure 3. Spatial variation in composition (cumulative percent weight) of predators' diets. (NSQF = northern squawfish, WAL = walleye, SMB = smallmouth bass, and CHC = channel catfish).

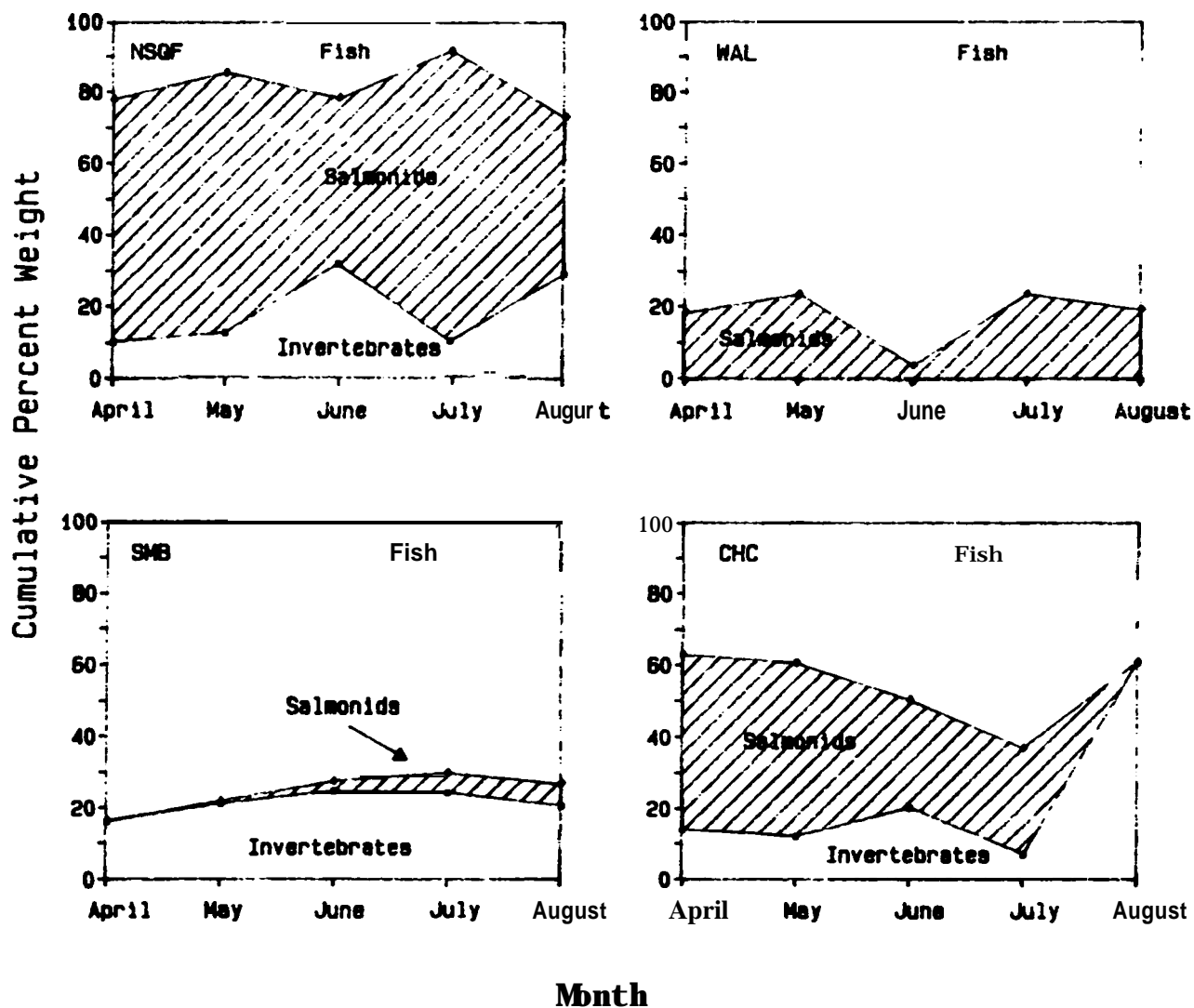


Figure 4. Seasonal variation in composition (cumulative percent weight) of predators' diets. (NSQF = northern squawfish, WAL = walleye, SMB = smallmouth bass and CHC = channel catfish).

44% and northern squawfish again switched to non-salmonid fishes, primarily cottids and American shad, an anadromous species with the peak emigrations of juveniles occurring in August and September.

The importance of fish in the diet northern squawfish (by weight) increased with predator length (Figure 5). Ephemeropteran and hymenopterian insects were the most important food items (41.2 - 90.5%) of northern squawfish less than 200 mm in length. Northern squawfish greater than 200 mm and less than 350 mm switched to crayfish and fish. Fish were the most important food items of predators 350 mm to 475 mm and ranged from 66 to 94% of the diet (by weight). Salmonids comprised 21% (by weight) of the diet of northern squawfish 300mm in length and 83% of the diet of northern squawfish 475 mm in length.

Walleye - Of the 1051 walleye collected (145-816 mm FL), 50% had food in their stomachs; 32 taxa of prey, comprising five major groups were consumed (Table 3). Diet composition of walleye varied little among sampling areas and years, therefore data were pooled for the whole reservoir 1983-1986. Most walleyes (97%) were collected at the McNary Dam tailrace and Irrigon stations in the reservoir; only 27 walleyes were collected at Arlington and none in the John Day Dam forebay. Fish comprised almost 100% of the weight of food items consumed by walleyes at all stations (Figure 3). Suckers were the most important prey, contributing 33-50% of the diet, followed by prickly sculpins (12-23%) and sandrollers (10-22%). Salmonids comprised 15, 10, and 39% of the diet at McNary, Irrigon, and Arlington; the higher percentage at Arlington may reflect a small sample size. Steelhead accounted for 4% of the diet at McNary, 0.1% at Irrigon and 0.0% at Arlington.

Although food habits differed slightly among reservoir stations, monthly differences were evident (Figure 4). Suckers were the most important food (by weight) of walleyes during April, May, June, and August (30-51%), but during July walleye switched to sandrollers (46%). Sandrollers were the second most important food in the diet of walleyes during June and August (24 and 24%), but contributed relatively little to the diet during April and May (1 and 6%). Sculpins were common during April (29%) and May (22%), but were of less importance thereafter (10-17%). Salmonids consistently contributed 18-24% of the diet (by weight), except for June (4%) when the abundance of migrants was relatively low. No steelhead were found in walleye stomachs during April, but they represented 3.5 and 2.4% of the diet during May and June.

Fish were by far the most important food of all sizes of walleyes (200-800 mm) (Figure 5). Salmonids were the most important preyfish of walleyes less than 300 mm (27-60%) in length, and frequently were of secondary importance for larger predators. Steelhead contributed 4 and 8% to the diet of walleye 550-650 mm, but were not found in the stomach contents of smaller walleyes. Sandrollers were the dominant food items

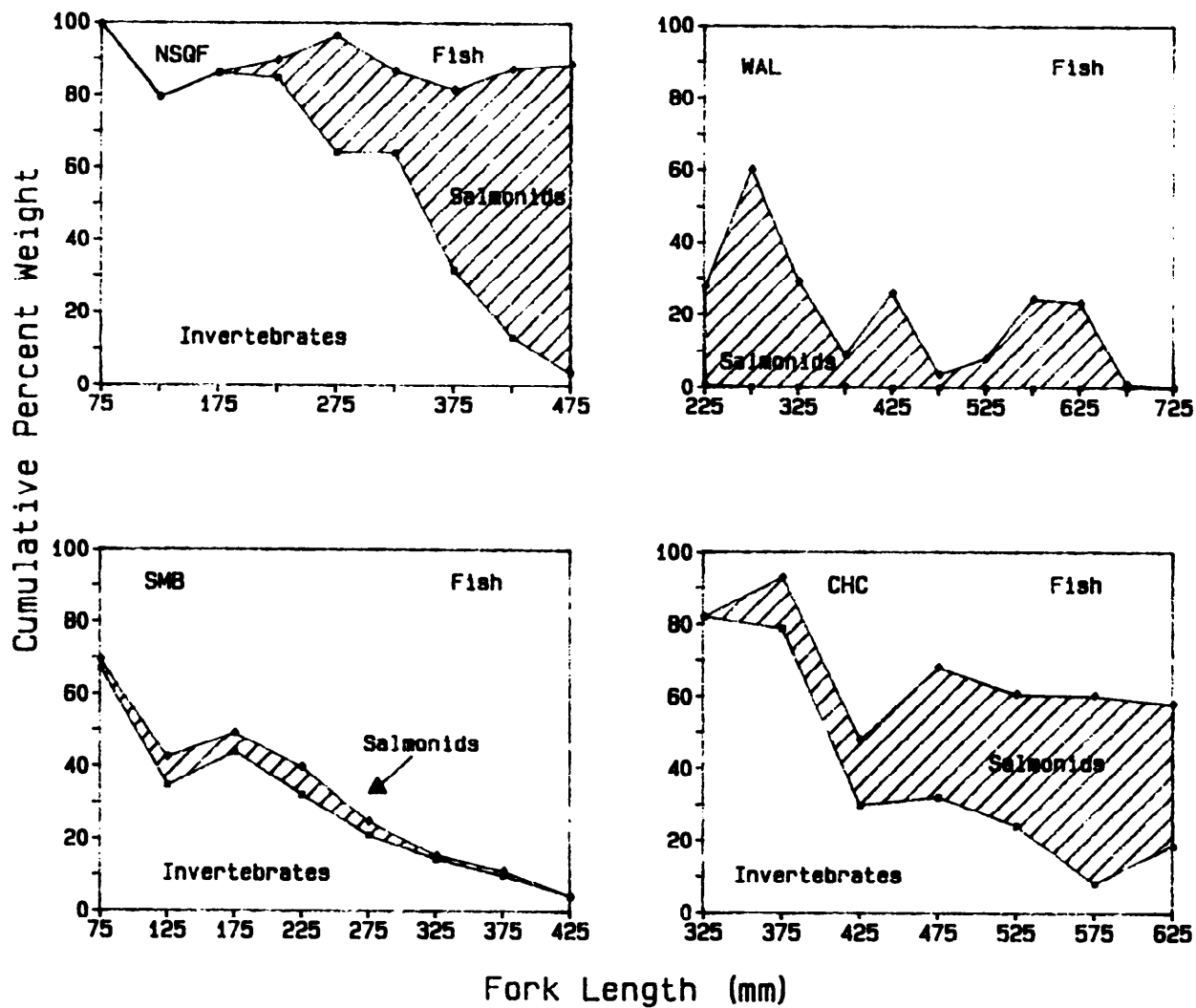


Figure 5. Variation in composition (cumulative percent weight) of predators' diets with different predator lengths. (NSQF = northern squawfish, WAL = walleye, SMB = smallmouth bass, and CHC = channel catfish).

of walleyes 350-550 mm in length (34-36%) whereas suckers were the most important prey item of walleyes greater than 550 mm (34-83%).

Smallmouth Bass - Of the 4,811 smallmouth bass collected (50-583 mm FL), 82% had food in their stomachs; 46 taxa of prey items, comprising five major groups were consumed (Table 3). Food habits of smallmouth bass varied among reservoir areas (Figure 3). Fish comprised 96% of the diet at McNary and Irrigon, but only 72 and 62% at Arlington and John Day Dam forebay, respectively. Prickly sculpin was the most important food item in the diet of smallmouth bass at McNary Dam, Irrigon, and Arlington (34-43%). In contrast, invertebrates, mainly crayfish increased in importance in the diet (by weight) from upstream to downstream: McNary (2%); Irrigon (3%); Arlington (26%); and John Day Dam forebay (36%). At John Day Dam forebay where crayfish were the dominant food item, chiselmouth were the second most important food item (22%) and sculpins third in importance (19%). Salmonids were consumed at all stations consistently contributing a small proportion (2 - 5%) of the diet. Steelhead were found only in the stomach contents of smallmouth bass at John Day Dam forebay and comprised 0.2% of the diet.

The importance of various food items in the diet varied little between months (Figure 4). However, the importance of salmonids in the diet steadily increased from April through August (0 - 6%). The importance of major food items in the diet changed with length of smallmouth bass (Figure 5). Crustaceans (crayfish and amphipods) were the most important food item of smallmouth bass 50 to 100 mm in length, accounting for 57% of the diet. Smallmouth bass greater than 100 mm in length began switching to fish as the major dietary component and crayfish decreased in importance with increasing predator size. Crayfish were the single most important food item in the diet of smallmouth bass less than 250 mm, but prickly sculpins were the most important prey of predators 250 - 399 mm in length (31 - 49%). Suckers were the most important food item (52%) of smallmouth bass greater than 400 mm. The importance of salmonids in the diet varied little with predator size; no identifiable steelhead were found in smallmouth less than 350 mm.

Channel Catfish - Of the 655 channel catfish collected (166-718 mm FL) 77% had food in their stomachs; prey consumed included 38 taxa of prey comprised in six major groups (Table 3). Almost 70% (452) of the channel catfish were collected in McNary Dam tailrace with 149 at Irrigon, 52 at Arlington and 2 at John Day Dam forebay. Salmonids were most important in the diets of channel catfish in McNary Dam tailrace where they made up about 60% of the diet (Figure 3). On a seasonal basis, salmonids were consumed as a significant dietary component from April (49%) through July (35%) with none consumed in August (Figure 4). The importance of salmonids also apparently increased with predator length (Figure 5) with channel catfish switching from crayfish to fish at about 400 mm and catfish longer than 475 mm consuming higher proportion of salmonids.

Prey Species Selection

Predator preference and selection for each prey fish type was inferred by comparing the proportion of that prey in the diet (r) versus the proportion of the same prey available in the environment (p) during April, May, June, and August, 1984 and 1985. Selection of prey fish species by northern squawfish changed by month and reservoir location (Table 4). Although salmonids were relatively low in abundance in the environment compared to suckers and sandrollers, northern squawfish diets showed a preference for salmonids. This was most evident during the peak spring period of the smolt emigration in May and again during a high emigration period of sub-yearling chinook in August; Ivlev's E_i values dropped in June during the transition in smolt species composition when juvenile salmonid abundance decreased. Prickly sculpin was generally the second most preferred prey fish and was selected by northern squawfish in the upper and middle reservoir (Table 4). In June sculpins were the most preferred prey fish in the upper and middle reservoir, coinciding with the lower smolt abundance. Suckers and sand-rollers were almost always selected against, although they were very abundant in the reservoir. When juvenile American shad became available to northern squawfish in August, they were usually a common prey item in the mid and lower reservoir.

Although salmonids were selected for, they were not a preferred prey fish in the diet of walleyes, except during August (Table 5). Sculpins were the preferred prey fish throughout the year and although suckers and sandrollers were important components of the diet, they were only randomly selected.

Smallmouth bass tended to select against salmonids in all months and reservoir locations with the exception of August in the lower reservoir when subyearling chinook salmon were a preferred prey (Table 6). Prickly sculpins were highly selected for in all areas of the reservoir throughout the year except in April and May in the lower reservoir when sandrollers were an important prey fish.

Prey Size Selection

The monthly prey size preference by northern squawfish in the BRZ generally followed the mean size of smolts passing McNary dam, except in May and August when squawfish preferred smolts of a smaller mean length than was available (Figure 6). The mean size of smolts was largest in April and May when the smolt migration was comprised largely of yearling chinook and steelhead and decreased as smaller subyearling chinook comprised an increasing proportion of the migration during June and almost totally dominated the migration in July and August. During May, northern squawfish fed less at random upon available prey and the length distribution of salmonids in the stomach contents and environment were not significantly correlated ($R^2 = 0.520$). As the mean size of smolts

Table 4. Monthly electivity values (E_i) of major prey fishes selected by northern squawfish as calculated from r (relative proportions of prey fish in the gut) and p, (relative proportions of prey fish available in the upper (McNary Dam tailrace and Irrigon), middle (Arlington), and lower (John Day Dam forebay) sections of John Day reservoir), 1984 and 1985 combined.

Reservoir Area	Prey Fish	April			May			June			August		
		r	p	E_i	r	p	E_i	r	p	E_i	r	p	E
Upper	salmon	13.3	4.4	0.50	49.0	6.8	0.75	9.4	16.5	-0.27	18.7	0.3	0.97
	steelhead	0.0	0.1	-1.00	3.8	0.0	1.00	3.1	0.0	1.00	0.0	0.0	-
	suckers	6.7	55.8	-0.79	1.9	28.7	-0.87	9.4	25.1	-0.46	31.2	18.2	0.26
	sculpins	60.0	3.5	0.89	27.9	3.8	0.76	53.1	5.5	0.82	31.2	3.3	0.81
	minnows	0.2	11.2	-0.96	0.0	20.0	-1.00	0.0	14.2	-1.00	12.5	16.5	-0.14
	sandrollers	0.0	24.9	-1.00	17.3	40.6	-0.40	25.0	38.7	-0.21	6.3	29.8	-0.65
	shad	0.0	0.0	-	0.0	0.0	-	0.0	0.0	-	0.0	31.8	-1.00
Middle	salmon	33.3	9.6	0.55	29.1	10.0	0.49	38.1	15.3	0.43	12.5	1.3	0.81
	steelhead	11.1	0.6	0.90	25.0	0.3	0.98	4.8	0.3	0.90	0.0	0.3	-1.00
	suckers	5.6	35.6	-0.73	8.3	58.0	-0.75	4.8	55.2	-0.84	4.2	51.5	-0.85
	sculpins	38.9	9.4	0.61	37.5	18.9	0.33	47.6	0.7	0.97	16.7	2.7	0.72
	minnows	5.6	6.9	-0.10	0.0	2.7	-1.00	4.8	1.5	0.52	4.2	33.0	-0.77
	sandrollers	5.6	38.0	-0.74	0.0	10.4	-1.00	0.0	27.0	-1.00	4.2	8.1	-0.32
	shad	0.0	0.0	-	0.0	0.0	-	0.0	0.0	-	58.3	3.0	0.90

Table 4. (continued)

Reservoir Area	Prey Fish	April			May			June			August		
		r	p	E _i	r	p	E _i	r	p	E _i	r	p	E _i
Lower	salmon	67.2	2.4	0.93	57.1	1.4	0.95	50.0	1.4	0.93	26.3	0.6	0.96
	steelhead	17.2	1.2	0.87	14.3	0.4	0.95	0.0	0.2	-1.00	0.0	0.1	-1.00
	suckers	1.7	33.6	-0.90	0.0	41.5	-1.00	20.0	50.6	-0.43	3.5	26.1	-0.76
	sculpins	12.1	46.2	-0.58	11.4	29.3	-0.44	10.0	12.5	-0.11	1.7	8.6	-0.66
	minnows	0.0	15.7	-1.00	17.1	25.6	-0.20	20.0	34.6	-0.27	1.7	16.0	-0.81
	sandrollers	1.7	0.9	0.32	0.0	1.8	-1.00	0.0	0.2	-1.00	0.0	1.1	-1.00
	shad	0.0	0.0	-	0.0	0.0	-	0.0	0.0	-	66.7	47.4	0.17

Table 5. Monthly electivity values (E_i) of major prey fishes selected by walleye as calculated from r (relative proportions of prey fish in the gut) and p , (relative proportions of prey fish available in the upper (McNary Dam tailrace and Irrigon), middle (Arlington), and lower (John Day Dam forebay) section of John Day reservoir), 1984 and 1985.

Reservoir Area	Prey Fish	April			May			June			August		
		r	p	E_i	r	p	E_i	r	p	E_i	r	p	E_i
Upper	salmon	10.9	4.4	0.43	16.4	6.8	0.41	3.5	16.5	-0.65	14.8	0.3	0.96
	steelhead	0.0	0.1	-1.00	2.1	0.0	1.00	0.4	0.0	1.00	0.0	0.0	-
	suckers	29.1	55.8	-0.31	20.1	28.7	-0.18	20.0	25.1	-0.11	18.5	18.2	0.01
	sculpins	43.6	3.5	0.85	32.8	3.8	0.79	13.1	5.5	0.41	22.2	3.3	0.74
	minnows	5.4	11.2	-0.35	9.0	20.0	-0.38	5.4	14.2	-0.45	14.8	16.5	-0.05
	sandrollers	10.9	24.9	-0.39	19.6	40.6	-0.35	57.7	38.7	0.20	29.6	29.8	-0.01
	shad	0.0	0.0	-	0.0	0.0	-	0.0	0.0	-	0.0	31.8	-1.00

Table 6. Monthly electivity values (E_i) of major prey fishes selected by smallmouth bass as calculated from r (relative proportions of prey fish in the gut) and p , (relative proportions of prey fish available in the upper (McNary Dam tailrace and Irrigon), middle (Arlington), and lower (John Day Dam forebay) section of John Day reservoir), 1984 and 1985.

Reservoir Area	Prey Fish	April			May			June			August		
		r	p	E_i	r	p	E_i	r	p	E_i	r	p	E
Upper	salmon	0.0	4.4	-1.00	0.0	6.8	-1.00	3.2	16.5	-0.67	0.3	0.3	-
	steelhead	0.0	0.1	-1.00	0.0	0.0	-	0.0	0.0	-	0.0	0.0	-
	suckers	1.9	55.8	-0.93	15.4	28.7	-0.30	26.7	25.1	0.03	33.2	18.2	0.35
	sculpins	88.7	3.5	0.92	70.3	3.8	0.90	45.6	5.5	0.78	33.8	3.3	0.82
	minnows	0.0	11.2	-1.00	2.2	20.0	-0.80	1.8	14.2	-0.77	21.3	16.5	0.13
	sandrollers	9.4	24.9	-0.45	12.1	40.6	-0.54	22.6	38.7	-0.26	6.4	29.8	-0.65
	shad	0.0	0.0	-	0.0	0.0	-	0.0	0.0	-	0.0	31.8	-1.00
Middle	salmon	0.0	9.6	-1.00	3.5	10.0	-0.49	2.8	15.3	-0.69	0.9	1.3	-0.18
	steelhead	0.0	0.6	-1.00	0.0	0.3	-1.00	0.0	0.3	-1.00	0.0	0.3	-1.00
	suckers	19.8	35.6	-0.28	15.9	58.0	-0.57	28.0	55.2	-0.33	50.2	51.5	-0.01
	sculpins	68.6	9.4	0.76	72.6	18.9	0.59	48.1	0.7	0.97	41.3	2.7	0.88
	minnows	1.2	6.9	-0.70	3.5	2.7	0.13	2.8	1.5	0.30	1.4	33.0	-0.92
	sandrollers	10.5	38.0	-0.57	4.4	10.4	-0.39	18.2	27.0	-0.19	5.2	8.1	-0.22
	shad	0.0	0.0	-	0.0	0.0	-	0.0	0.0	-	0.9	3.0	-0.53

Table 6. (continued)

Reservoir Area	Prey Fish	April			May			June			August		
		r	p	E _i	r	p	E _i	r	p	E _i	r	p	E _i
40 Lower	salmon	2.2	2.4	-0.05	0.7	1.4	-0.34	0.0	1.9	-1.00	9.1	0.6	0.88
	steelhead	0.0	1.2	-1.00	0.0	0.4	-1.00	0.8	0.2	0.6	0.0	0.1	-1.00
	suckers	21.7	33.6	-0.21	19.7	41.5	-0.36	13.5	50.6	-0.58	9.1	26.1	-0.48
	sculpins	28.3	46.2	-0.24	37.3	29.3	0.12	57.1	12.5	0.64	65.7	8.6	0.77
	minnows	41.3	15.7	0.45	40.8	25.6	0.23	26.2	34.6	-0.14	13.1	16.0	-0.10
	sandrollers	6.5	0.9	0.76	1.4	1.8	-0.12	2.4	0.2	0.86	3.0	1.1	0.46
	shad	0.0	0.0	-	0.0	0.0	-	0.0	0.0	-	0.0	47.4	-1.00

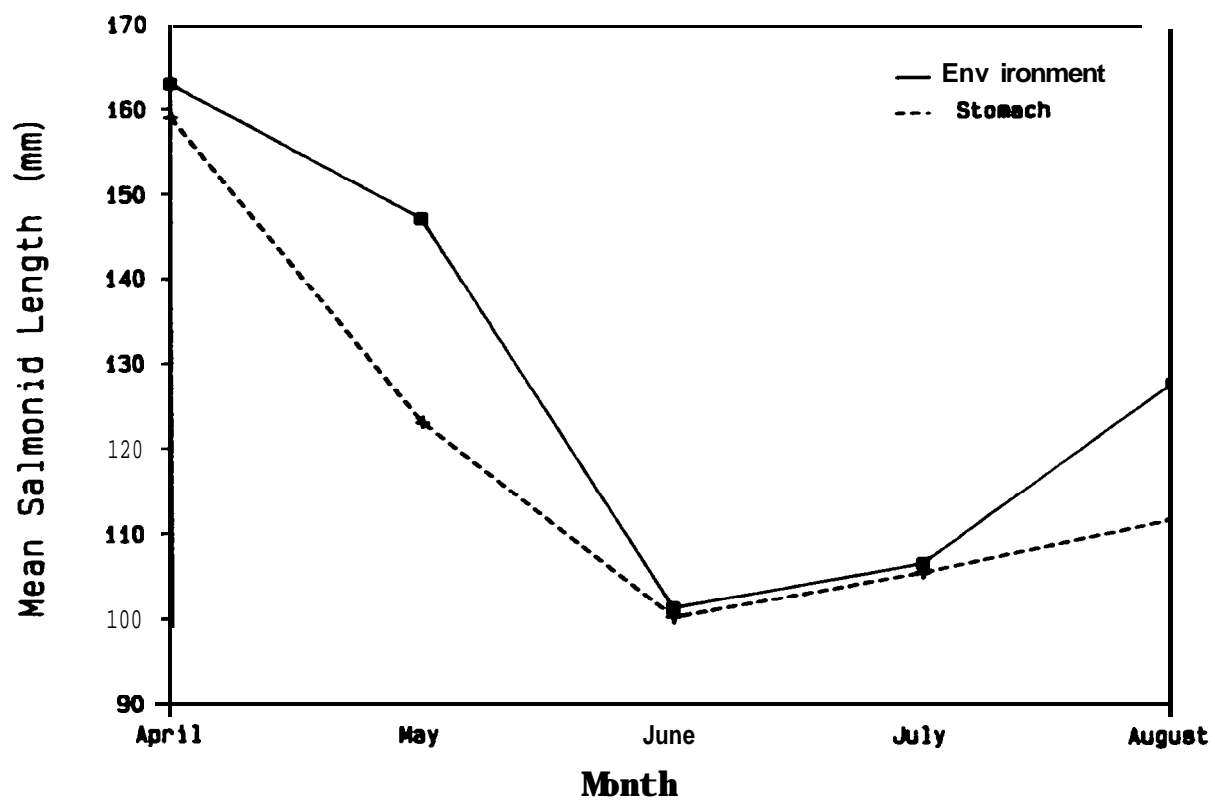


Figure 6. Seasonal variation in mean lengths of juvenile salmonids consumed by northern squawfish compared to those in the environment (passing McNary Dam), 1983-1986.

decreased, however, the length distribution of smolts in the stomach contents and in the migration became significantly correlated during June ($R^2 = 0.7831$ and July ($R^2 = 0.9491$).

The maximum size of salmonid prey vulnerable to northern squawfish predation increased linearly with predator length ($R^2 = 0.96$) (Figure 7). During 1983 through 1986, the maximum size of salmonids consumed by northern squawfish 220 mm in length was 82 mm, whereas predators 40 mm in length consumed salmonids up to 250 mm in length (Figure 7). The number of salmonids in the migration vulnerable to predation varied with the size of predator and the seasonal distribution of smolt size (Table 7). For example, in April 22.8% of the available salmonids were vulnerable to northern squawfish 300 mm in length, but 89.3% were vulnerable to predators 400 mm long. In contrast, during July, 96.2% of the juvenile salmonids were vulnerable to predators 300 mm in length and virtually all juvenile salmonids could possibly have been eaten by 350 mm northern squawfish. Subyearling chinook were most vulnerable to northern squawfish predation with almost all fish being vulnerable to predators 250-20 mm in length, whereas yearling chinook and the larger steelhead became vulnerable with increasing predator length (Table 7).

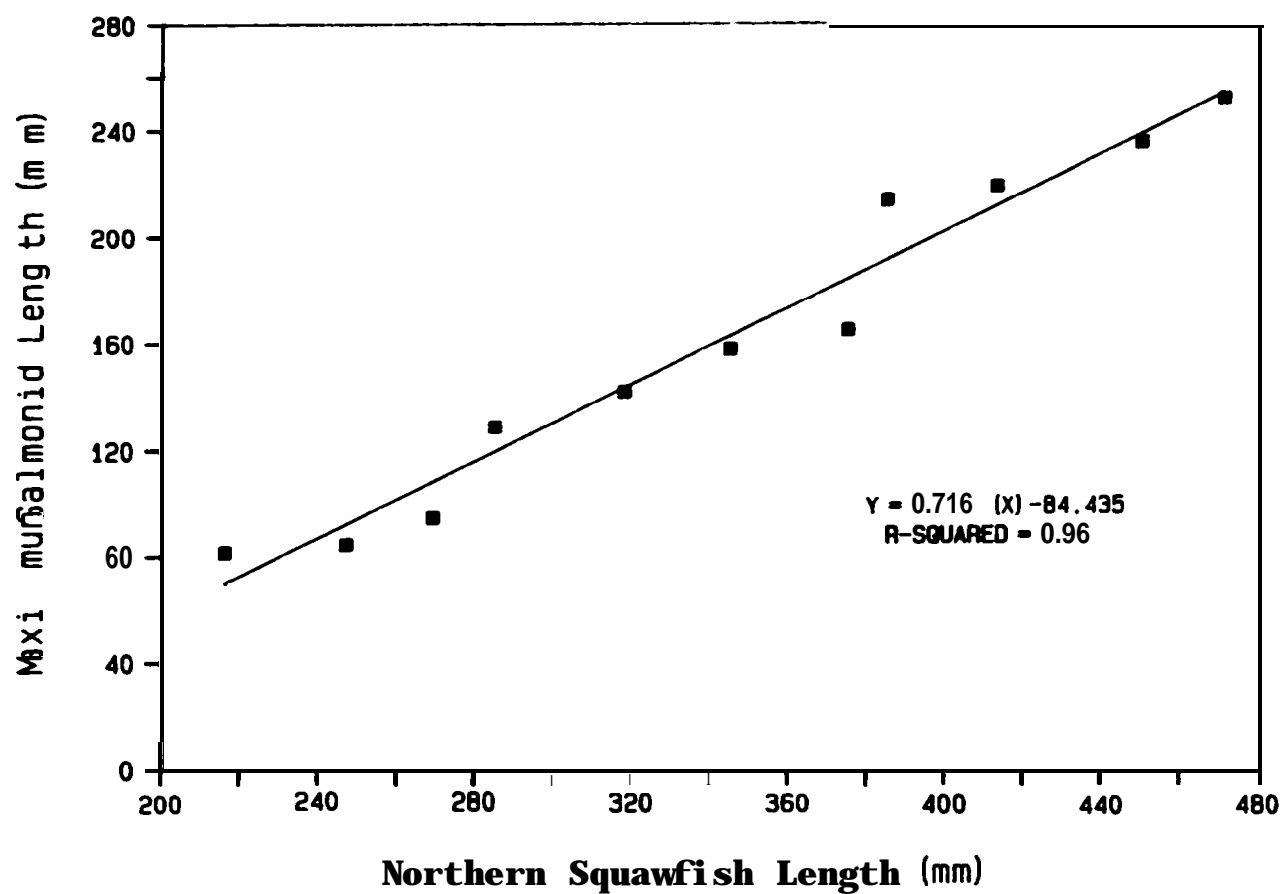


Figure 7. Relationship of the maximum size of juvenile salmonids consumed by northern squawfish to northern squawfish fork length, 1983-1986.

Table 7. Percent of available salmonids* vulnerable to predation by various sizes of northern squawfish from April-August, 1983-1986, at McNary Dam, boat restricted zone, John Day Reservoir.

Length(mm)		Month				
Predator	Maximum Prey	April	May	June	July	August
200	59	0.2	0.1	11.6	0.0	0.0
225	77	0.2	0.1	13.6	0.2	0.0
250	95	2.6	2.1	29.2	4.5	0.1
275	112	12.2	12.8	73.7	68.9	13.4
300	130	22.8	29.1	87.9	96.2	56.2
325	148	28.1	44.0	91.4	98.6	81.0
350	166	37.8	72.6	94.9	99.9	98.8
375	184	59.5	84.9	96.6	100.0	99.9
400	202	89.3	91.4	97.5	100.0	100.0
425	220	97.6	95.7	98.7	100.0	100.0
450	238	99.1	97.5	99.1	100.0	100.0
475	256	100.0	100.0	100.0	100.0	100.0
500	274	100.0	100.0	100.0	100.0	100.0

* Salmonids = yearling and subyearling chinook, sockeye, and coho salmon and steelhead.

DISCUSSION

Significance of Smolts in Predators' Diets

Of the four predator species studied, only northern squawfish utilized juvenile salmonids as a significant food resource during smolt emigrations through John Day Reservoir. This was especially true for northern squawfish during the migratory peaks of yearling chinook and steelhead in May and for subyearling chinook in July. This finding is not surprising as northern squawfish have been documented as "serious" predators on juvenile salmonids on many occasions (Ricker 1933, 1941; Foerster and Ricker 1941; Thompson 1959; Thompson and Tufts 1967; Eggers et al. 1978; Sims et al. 1977, 1978; and Urernovich et al. 1980). There have also been a number of cases where juvenile anadromous salmonids were available but were not significantly preyed upon by northern squawfish (Casey 1962; Falter 1969; Moyle 1976; Buchanan et al. 1981; and Kirn et al. 1986). As Brown and Moyle (1981) aptly point out, most of the cases where northern squawfish have consumed large numbers of juvenile salmonids have been in either lakes containing large squawfish populations or artificial environments or situations (i.e. near hydroelectric projects or hatchery release sites). We also found that the areas near the dams (i.e. the BRZ at McNary Dam and the forebay area at John Day Dam) were the locations where northern squawfish predation on juvenile salmonids appeared most intense. This pattern may have occurred because juvenile salmonids are concentrated into smaller areas at the dams because of delayed passage (Sims et al. 1981) and restricted entry ways and outlets. Many smolts are also disoriented during passage and washed back to the dam face into slackwater areas (Long et al. 1968) where smolts have been observed to be preyed upon by schools of squawfish at the surface (Brad Eby USACOE and Paul Wagner WDG, personal communications). These slackwater areas have also been documented as preferred sites of distribution for northern squawfish (Faler et al. 1988). There may also be a numerical response of northern squawfish to the increased concentrations of smolts below the dam because northern squawfish abundance is from 6 to 30 times higher in the BRZ than the remainder of the reservoir (Beamsderfer and Rieman 1988).

An alternative explanation for the high percentage of smolts in diets of northern squawfish just below the McNary Dam might be that they are preying on smolts killed or severely injured during turbine passage. However, this does not explain the comparable percentage of smolts consumed by northern squawfish in John Day Dam forebay. We also found only three instances in over 4,000 squawfish stomachs where freshly ingested smolts appeared to be physically injured (i.e. clearly severed pieces) from turbine passage (U.S. Fish and Wildlife Service, unpublished data).

Walleye was the third most important predator on juvenile salmonids and based on dietary composition (gravimetric) smolts made up 13.5% of

walleye diets over all years, months, and locations. Information on walleye predation on juvenile salmon or steelhead is rare because their natural range did not overlap that of Pacific salmonids. Maule and Horton (1984) is the only study where walleye has been documented as a predator on juvenile Pacific salmonids and their study was also conducted in John Day Reservoir. Their results were similar to ours indicating that prickly sculpin and suckers were the most important prey of walleye and juvenile salmonids only comprised 3.6% (by volume) of walleye diets.

Diet composition indicated that smallmouth bass was the least important predator on smolts (3.7% overall) emigrating through John Day Reservoir. Only in July and August were juvenile salmonids present in smallmouth bass diets and this was most likely due to subyearling chinook inhabiting littoral areas of the river (Dawley et al. 1986) where they likely overlap the distribution of smallmouth bass (Beamsderfer and Rieman 1988). In other instances where juvenile salmonids and smallmouth bass have overlapped their distributions (Lockner 1950; Martin and Fry 1972; and Bennett et al. 1983), smallmouth bass have not been an important predator on juvenile salmonids. However, in certain situations, such as right after hatchery releases (Warner 1972), during peak emigration densities (Pflug and Pauley 1983), and where juvenile salmonids are rearing in littoral areas which overlap preferred smallmouth bass habitat (Rondorf 1988) they may become important predators on juvenile salmonids.

Channel catfish was the second most important predator on juvenile salmonids comprising (gravimetric) 32.9 % of channel catfish diets over all years, months, and locations. Similar to walleye, channel catfish was another introduced species to the system and other than Bennett et al. (1983), there is no information available on channel catfish predation on smolts because their native ranges did not overlap. In Snake River reservoirs Bennett et al. (1983) found that about 41 % of all channel catfish collected in the spring in tailrace areas contained chinook salmon and steelhead smolts. Their results were similar to those from this study which indicated that almost all channel catfish predation on smolts occurred in the tailrace area and was mostly confined to the spring. This pattern may be due to the distribution pattern of channel catfish which appeared to congregate in the upper part of the reservoir in spring.

Prey Species Selectivity

A major objective of this study was to determine how predators' diets varied in response to the increase in prey density or abundance during the emigration of juvenile salmonids (> 10 million) thru the reservoir. An emigration such as this should increase encounter rates of predators with smolts (in overlapping habitats) and predators would be expected to switch to feed more selectively on prey (smolts) at higher densities than lower densities (Werner and Hall 1974, Charnov 1976, and Gardner 1981). Our diet composition data indicate that northern squawfish

and channel catfish, to a lesser degree, were the only predators which preferred juvenile salmonids more during their peak migratory densities (in May and July for northern squawfish and in May for channel catfish (Figure 5)). The predator electivity data were less clear cut in supporting this hypothesis and although the relative proportions of salmon and steelhead in the stomachs of northern squawfish (r) generally increased with increased migratory densities of juvenile salmonids, the E values did not vary in the same pattern because the prey (juvenile salmonid) availability, as measured by beach seine samples (p), did not follow juvenile salmonids migratory abundance trends. In other words, E_i values remained quite high (often near +1.00) throughout the migration season (showing preference for juvenile salmonids by northern squawfish) but did not vary much in relation to variation in densities of juvenile salmonids at different times during their migration. One explanation for the discrepancies between the availability data (p) of salmonids collected by beach seine and migration abundance data may be that, although beach seine samples were taken in the littoral areas of the reservoir where the northern squawfish were collected, these samples may have underestimated the relative abundance of juvenile salmonids in the reservoir which are considered to migrate more in the open water, mid-channel areas than in the littoral areas (Dawley et al. 1986). We, therefore, cannot rule out the possibility that northern squawfish were feeding on juvenile salmonids more in the main channel of the reservoir and then moving back into the littoral areas where we captured them.

Only in August did walleye and smallmouth bass select for salmonids. The reason for this was because the subyearling chinook, which comprised almost 100% of the juvenile salmonid out-migration at this time of the year, were probably rearing in the littoral areas of the reservoir at this time (Dawley et al. 1986) and their distribution pattern would overlap more with walleye and especially smallmouth bass.

Prey Size Selectivity

Our study results generally refute the hypothesis that northern squawfish (the only predator that could be tested for juvenile salmonid size selectivity) are size selective when feeding on juvenile salmonids. Only during May and August did northern squawfish feed less at random upon available salmonids and the mean length of salmonids in the stomach contents was smaller than the mean length in the environment and were not correlated. During May the mean length of salmon juveniles was smaller than the mean length of steelhead juveniles and this indicates that northern squawfish were selecting salmon over steelhead in May and it was probably size related selectivity. If this conclusion is correct one salmon management implication would be to increase the size of hatchery salmon (spring chinook) released in April and May to reduce predation losses due to northern squawfish.

Two studies that have examined lengths of juvenile salmonids consumed by northern squawfish, (Olney 1975 and Uremovich et al. 1980) found that salmonid lengths consumed by northern squawfish were similar to lengths of salmonids collected from the nearby environment. Thompson and Tufts (1967) however, found that northern squawfish switched from feeding on wild sockeye salmon fingerlings at a mean length of 59.6 mm to hatchery sockeye salmon fingerlings at a mean length of 97.7 mm. This switch, however, was more of a switch from northern squawfish feeding on small numbers (1% frequency in diet) of wild salmonids to increased numbers (37% frequency in diets) of recently released hatchery salmonids and size selection did not appear to influence predator feeding preference.

Conclusions

Based on the dietary composition and prey selectivity of the four predators studied, we conclude that northern squawfish appears to be the major potential predator on juvenile salmonids in John Day Reservoir. Channel catfish may also be an important predator on juvenile salmonids during the spring in the upper reservoir. Walleye and smallmouth bass (in the order of importance) appear to be much less significant predators on salmonids and only in August appear to selectively consume subyearling chinook when their distributions may overlap.

The major objectives of this paper were to analyze the dietary composition and dynamics of prey selectivity of the four predators studied and these objectives have been addressed in this paper. However, in order to determine the overall significance or impact of this predation on the juvenile salmonids migrating through John Day Reservoir one needs to know the consumption rates and abundance of predators. The three following papers in this series answer this need: Vigg et al. (1988) provides the estimates of consumption rates, feeding chronologies, and daily rations of predators; Beamesderfer and Rieman (1988) provides estimated abundance and distribution of predators; and Rieman et al. (1988) integrates predator consumption rates and abundance estimates to estimate total juvenile salmonid losses and mortality for John Day Reservoir.

LITERATURE CITED

- Beamesderfer, R.C., and B.E. Rieman. 1988. Predation by northern squawfish, walleye, smallmouth bass, and channel catfish in a mainstem Columbia River reservoir: III. Estimated abundance and distribution of predators. Transactions of the American Fisheries Society 000:0000-0000.
- Bennett, D.H. P.M. Bratovich, W. Knox, D. Palmer, and H. Hansel. 1983. Status of the warmwater fishery and the potential of improving warmwater fish habitat in the lower Snake reservoirs. Final Report to U.S. Army Corps of Engineers. Contract DACW68-79-C0057. University of Idaho, Department of Fish and Wildlife Resources, Moscow, ID.
- Bently, W.W. and H.L. Raymond. 1976. Delayed migrations of yearling chinook salmon since completion of Lower Monumental and Little Goose Dams on the Snake River. Transactions of the American Fisheries Society 105:422-424.
- Brooks, J.L., and S.I. Dodson. 1965. Predation, body size, and composition of plankton. Science. 150:28-35.
- Brown, L.R. and P.B. Moyle. 1981. The impact of squawfish on salmonid populations: a review. North American Journal of Fisheries Management 1:104-111.
- Buchanan, D.V., R.M. Hooton, and J.R. Moring. 1981. Northern squawfish (Pychocheilus oregonensis) predation on juvenile salmonids in sections of the Willamette River basin, Oregon. Canadian Journal of Fisheries and Aquatic Science 38:360-364.
- Carpenter, S-R. J.F. Kitchell, and J.H. Hodgson. 1985. Cascading trophic interactions and lake productivity-fish predation and herbivory can regulate lake ecosystems. Bioscience 35(10):634-639.
- Casey, O.E. 1962. The life history of the northern squawfish in Cascade Reservoir. Master's thesis. University of Idaho, Moscow, Idaho, USA.
- Chapman, D.W. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth century. Transactions of the American Fisheries Society 115:662-670.
- Charnov, E.L., 1976. Optimal foraging: attack strategy of a mantid. American Naturalist 110:141-151.

- Craig, J.A., and R.L. Hacker. 1940. The history and developnent of the fisheries of the Columbia River. U.S. Bureau of Fisheries Bulletin 49(32):133-215.
- Dawley, E.M. and eight co-authors. 1986. Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966-1983. U.S. Dep. of Commer. NOAA, National Marine Fishery Service, Seattle, WA. 256 pp. (Report to Bonneville Power Administration, Portland, OR., Contract DE-A179-84BP39652).
- Ebel, W. 1977. Panel 2: Fish passage problems and solutions-major passage problems. Pages 33-39 in E. Schwiebert (ed.) Columbia River Salmon and Steelhead. American Fisheries Society. Special Publication No. 10. Washington, D.C.
- Ebel, W.J., and H.L. Raymond. 1976. Effect of atmospheric gas saturation on salmon and steelhead trout of the Snake and Columbia rivers. United States National Marine Fisheries Review 38(7):1-14.
- Eggers, D.M., N.W. Bartoo, N.A. Richard, R.E.E Nelson, R.C. Wissmar, R.L. Burgner and A.H. Devol. 1978. The Lake Washington ecosystem: the perspective from the fish community and forage base. Journal of the Fisheries Research Board of Canada 35:1553-1571.
- Evans, D.J. 1977. Keynote address. Pages 1-19 in E. Schwiebert (ed.) Columbia River Salmon and Steelhead. American Fisheries Society. Special Publication No. 10. Washington, D.C.
- Faler, M.P., L.M. Miller, K.I. Welke. 1988. Effects of variation in flow on distributions of northern squawfish in the Columbia River below McNary Dam. North American Journal of Fisheries Management 8:30-35.
- Falter, C.M. 1969. Digestive rates and daily rations of northern squawfish in the St. Joe River, Idaho. Doctoral dissertation, University of Idaho, Moscow, Idaho, USA.
- Foerster, R.E. and W.E. Ricker. 1941. The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus Lake. Journal of the Fisheries Research Board of Canada 5:315-336.
- Gardner, M.B. 1981. Mechanisms of size selectivity by planktivorous fish: a test of hypotheses. Ecology 62:571-578.

- Hall, D.J., W.E. Cooper, and E.E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnology and Oceanography*. 15:839-928.
- Hansel, H.C., S.D. Duke, P.T. Lofy, and G.A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. *Transactions of the American Fisheries Society* (In Press).
- Hjort, R.C., B.C. Mundy, and P.L. Hulett. 1981. Habitat requirements for resident fishes in the reservoirs of the lower Columbia River. Final Report. U.S. Army Corps of Engineers. Contract No. DACW57-79-C-0067, 180 p. Portland, OR.
- Hrbacek, J. M. Dvorakova, and L. Prochazkova. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton assemblage. *Verh. Int. Ver. Theoret. Angew. Limnol.* 14:192-195.
- Ivlev, U.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, CT. 302 p.
- Jeppson, P.W., and W.S. Platts. 1959. Ecology and control of the Columbia squawfish in Northern Idaho lakes. *Transactions of the American Fisheries Society* 88:197-202.
- Johnson, F.H., and J.G. Hale. 1977. Interrelation between walleye (Stizostedion vitreum vitreum) and smallmouth bass (Micropterus dolomieu) in four northeastern Minnesota lakes, 1948-69. *Journal of the Fisheries Research Board of Canada* 34:1626-1632.
- Kirn, R.A., R.D. Ledgerwed, and R.A. Nelson. 1986. Increased abundance and the food consumption of northern squawfish (Ptychocheilus oregonensis) at river kilometer 75 in the Columbia River. *Northwest Science* 60: 197-200.
- Knight, R.L., F.J. Margraf, and R.T. Carline. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. *Transactions of the American Fisheries Society* 113:677-693.
- Lechowicz, M.J. 1982. The sampling characteristics of electivity indices. *Oecologia* (Berlin) 52:22-30.
- Lachner, E.A. 1950. Food, growth and habits of fingerling northern smallmouth bass, Micropterus dolomieu dolomieu Lacepede, in trout waters of western New York. *Journal of Wildlife Management* 14(1):50-55.

- Long, C.W., R.F. Krucma, and F.J. Ossiander. 1968. Research on fingerling mortality in Kaplan turbines, 1968. Progress Report, Bureau of Commercial Fisheries, Seattle, WA. 7 pp.
- MacLean, J. and J.J. Magnuson. 1977. Species interactions in percid communities. Journal of the Fisheries Research Board of Canada 34:1941-1951.
- Martin, N.V., and F.E.J. Fry. 1972. Lake Opeongo: effects of exploitation and introductions on the salmonid community. Journal of the Fisheries Research Board of Canada 29:795-805.
- Maule, A.G., and H.F. Horton. 1984. Feeding ecology of walleye. Stizostedion vitreum vitreum, in the mid-Columbia River, with emphasis on the interactions between walleye and juvenile anadromous fishes. National Marine Fisheries Service Fishery Bulletin 82(2):411-418.
- Moyle, P.B. 1976. Inland Fishes of California. University of California Press, Berkeley, California. USA.
- NPPC (Northwest Power Planning Council). 1984. Columbia River Basin-fish and wildlife program. Adopted November 15, 1982. Amended October 10, 1984. NPPC, Portland, Oregon
- NPPC (Northwest Power Planning Council). 1986. Salmon and steelhead losses in the Columbia River Basin. NPPC, Portland, Oregon.
- Olney, F.E. 1975. Life history and ecology of the northern squawfish, Ptychocheilus oregonensis (Richardson) in Lake Washington, M.S. thesis, University of Washington, Seattle, WA. 75 p.
- Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist 100:65-75.
- Parsley, M.J., D.E. Palmer, and R.W. Burkhardt. 1988. Variation in capture efficiency of a beach seine for small fishes. North American Journal of Fisheries Management (In Press).
- Pflug, D.E., and G.B. Pauley. 1983. Biology of smallmouth bass (Micropterus dolomieu) in Lake Sammamish, Washington. Northwest Science 58: 118-130.
- Raymond, H.L. 1968. Migration rates of yearling chinook salmon in the Columbia River. Transactions of the American Fisheries Society 97: 356-359.

- Raymond, H.L. 1969. Effect of John Day Reservoir on the migration rate of juvenile chinook salmon in the Columbia River. Transactions of the American Fisheries Society 98:513-514.
- Raymond, H.L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966-1975. Transactions of the American Fisheries Society 108:505-529.
- Raymond, H.L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River Basin. Transactions of the American Fisheries Society (In Press).
- Ricker, W.E. 1933. Destruction of sockeye salmon by predatory fishes. Biological Board of Canada. Pacific Progress Report 18: 3-4.
- Ricker, W.E. 1941. The consumption of young sockeye salmon by predaceous fishes. Journal of the Fisheries Research Board of Canada 5: 293-313.
- Rieman, B.E. R.C. Beamesderfer, L.J. Bledsoe, S. Vigg, and T.P. Poe. 1988. Predation by northern squawfish, walleye, smallmouth bass, and channel catfish in a mainstem Columbia River reservoir IV. Estimates of juvenile salmonid loss and mortality. Transactions of the American Fisheries Society 000:000-000.
- Rosentreter, 1977. Panel 4: role of hatchery fish: angling, biology, and genetics. Pages 79-83 in E. Schwiebert (ed.) Columbia River Salmon and Steelhead.-American Fisheries Society. Special Publication No. 10. Washington, D.C.
- Ruggerone, G.T. 1986. Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. Transactions of the American Fisheries Society 115: 736-742.
- Seaburg, K.G. 1957. A stomach sampler for live fish. Progressive Fish Culturist 19: 137-139.
- Sims, C.W., W.W. Bentley, and R.C. Johnsen. 1977. Effects of power peaking operations on juvenile salmon and steelhead trout migrations-progress 1976. Report to the U.S. Army Corps of Engineers. National Marine Fisheries Service, Northwest Fisheries Center, Seattle, Washington. USA.
- Sims, C.W., W.W. Bentley, and R.C. Johnsen. 1978. Effects of power peaking operations on juvenile salmon and steelhead trout migrations-progress 1977. Report to the U.S. Army Corps of Engineers. National Marine Fisheries Service. Northwest Fisheries Center, Seattle, Washington, USA.

- Sims, C.W., J.G. Williams, D.A. Faurot, R.C. Johnsen, and D.A. Brege. 1981. Migrational characteristics of juvenile salmon and steelhead in the Columbia River basin and related passage research at John Day Dam, Volumes I and II. Report to the United States Army Corps of Engineers. United States National Marine Fisheries Service. Northwest and Alaska Fisheries Center, Seattle, Washington, USA.
- Schwiebert, E. (editor). 1977. Columbia River salmon and steelhead. American fisheries Society. Special Publication No. 10. Washington, D.C. 214 pp.
- Stevens, R.E. 1959. The white and channel catfishes of the Santee-Cooper reservoir and tailrace sanctuary. Thirteenth Ann. Conf. S.E. Assoc. Game and Fish Comm., Proc. pp 203-219.
- Stewart, D.J., J.F. Kitchell, and L.B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Transactions of the American Fisheries Society 110:751-763.
- Stone, L. 1878. The salmon fisheries of the Columbia River. Pages 801-823 in Report of the U.S. Bureau of Fisheries, 1875-1876, Washington, D.C.
- Thompson, R.B. 1959. Food of the squawfish Ptychocheilus oregonensis (Richardson) of the lower Columbia River. United States Fish and Wildlife Service, Fishery Bulletin 158:43-58.
- Thompson, R.B., and D.F. Tufts. 1967. Predation by Dolly Varden and northern squawfish on hatchery-reared sockeye salmon in Lake Wenatchee, Washington. Transactions of the American Fisheries Society 96:424-427.
- Trefethen, P. 1972. Man's impact on the Columbia River. Pages 77-98 in R.T. Oglesby, C.A. Carlson, and J.A. McCann (eds.) River Ecology and Man. Academic Press, New York and London.
- Uremovich, B.L., S.P. Cramer, C.F. Willis, and C.O. Junge. 1980. Passage of juvenile salmonids through the ice-trash sluiceway and squawfish predation at Bonneville Dam, 1980. Oregon Department of Fish and Wildlife, Clackamas, OR (Report to U.S. Army Corps of Engineers, Portland, OR).
- Vigg, S., T.P. Poe, L.A. Prendergast, and H.C. Hansel. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: II. Consumption rates of northern squawfish, walleye, smallmouth bass, and channel catfish. Transactions of the American Fisheries Society 000:000-000.
- Valiela, I. 1984. Marine ecological processes. Springer-Verlag. New York. 546 pp.

- Vanderploeg, H.A. and D. Scavia. 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. *Ecological Modelling* 7:135-149.
- Wagner, W.C. 1972. Utilization of alewives by inshore piscivorous fishes in Lake Michigan. *Transactions of the American Fisheries Society* 101:55-63.
- Weitkamp, D.E., and M. Katz. 1980. A review of dissolved gas supersaturation literature. *Transactions of the American Fisheries Society*. 109:659-702.
- Werner, E.E. and D.J. Hall. 1974. Optimal foraging and the size selection prey by the bluegill sunfish (Lepomis macrochirus). *Ecology* 55: 1042-1052.
- Zaret, T.M., and T.R. Paine. 1973. Species introduction in a tropical lake. *Science* 152:449-455.
- Zaugg, W.S., E.F. Prentice, and F.W. Waknitz. 1985. Importance of river migration to the development of seawater tolerance in Columbia River darters. *Aquaculture* 51:33-47.

PREDATION BY RESIDENT FISH ON JUVENILE SALMONIDS IN A MAINSTEM
COLUMBIA RIVER RESERVOIR:

PART II. CONSUMPTION RATES OF A NORTHERN SQUAWFISH, WALLEYE, SMALLMOUTH BASS,
AND CHANNEL CATFISH

by

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Abstract

Adult northern squawfish (Ptychocheilus oregonensis), walleye (Stizostedion vitreum vitreum), smallmouth bass (Micropterus dolomieu), and channel catfish (Ictalurus punctatus) were sampled from four regions of John Day Reservoir, Columbia River during April-August 1983-1986 to quantify consumption rates on 13 species of juvenile prey fish. The primary objective was to determine consumption rates on seaward migrating juvenile Pacific salmon (Oncorhynchus spp.) and steelhead (Salmo gairdneri) in reference to the hydropower system. Consumption rates were estimated by integrating in situ stomach contents data with laboratory determined digestion rate relations. Abiotic and biotic conditions which could affect consumption rates were relatively constant among the four years of the study, therefore data were combined over years for consumption rate estimates. For each predator, consumption rates varied by reservoir area, month, time of day, and predator size (age). Northern squawfish congregated below McNary Dam during periods of peak juvenile salmonid migration, and exhibited the greatest mean seasonal consumption rates in this area, i.e., $0.7 \text{ prey } \cdot \text{predator}^{-1} \cdot \text{d}^{-1}$. Mean seasonal salmonid consumption by channel catfish was also high in McNary Tailrace (0.5); while that by walleye (0.2) and smallmouth bass (0.04) occurred predominantly in the mid to lower reservoir. Maximum consumption rates of all predators generally occurred in July, concurrent with maximum temperature and juvenile salmonid abundance. Diel feeding chronology of the predators was generally bimodal -- with active feeding apparent after dawn (0600-1200), and another mode at night (2000-2400 hours). Northern squawfish in the McNary Dam tailrace exhibited this bimodal pattern, but in the remainder of the reservoir feeding was primarily at dawn and morning hours. Daily ration of salmonids and total prey fish ($\text{mg prey} \cdot \text{g predator}^{-1} \cdot \text{d}^{-1}$) generally increased to a peak at a predator-specific age with a subsequent decline. Maximum daily ration of total prey fish for northern squawfish ($14.0 \text{ mg } \cdot \text{g}^{-1}$) occurred at age 13, in contrast to the other predators which had higher fish rations at much younger ages: walleye (38.81 age 1; smallmouth bass (27.4) age 3; and, channel catfish (16.0) age 7. Mean seasonal daily ration (all food items) of smallmouth bass ($28.7 \text{ mg } \cdot \text{g}^{-1}$) was about twice that of the other predators: channel catfish, 12.6; northern squawfish, 14.1; and walleye, 14.2. All four predators studied were highly piscivorous, however, the evidence presented in this study indicates that northern squawfish was the major predator on juvenile salmonids during 1983-1986.

Introduction

Knowledge of food consumption rates of the piscivores in a fish community is fundamental to an understanding of the predator-prey relations, processes causing population dynamics, and trophic ecology of an aquatic system. Consumption estimates for all major predators are important parameters for multi-species trophodynamic models since daily ration influences the amount of energy available to the consumer for growth and determines the effect a consumer population has on the dynamics of prey and competitor populations (Sainsbury 1986). During 1983-1986, adult northern squawfish, walleyes, smallmouth bass, and channel catfish were sampled from John Day Reservoir, Columbia River to determine consumption on 13 species of juvenile prey fish -- with primary emphasis on out-migrating juvenile salmonids (Table 1). In situ stomach contents data, stratified on a spatio-temporal basis, were integrated with laboratory determined digestion rate relations in order to estimate daily consumption rates.

Estimation of fishes' food consumption in nature from the quantity of food present in the stomach and models of evacuation (retention) rate of stomach contents was first proposed by Bajkov (1935), and has been an active area of biological research during the past 20 years (see Windell 1967; Davis and Warren 1968; Brett and Higgs 1970; Swenson and Smith 1973; Doble and Eggers 1978; Elliot and Persson 1978; Mann 1978; Fange and Grove 1979; Jobling 1981, 1986; and, Persson 1982, 1986 for seminal papers and reviews). The method used in this study to estimate consumption rates, herein referred to as "Swenson's technique", was modified from the work of Swenson (1972) and Swenson and Smith (1973). Swenson's technique reconstructs an average diel feeding pattern from pooled stomach contents of a sample of predators collected under natural conditions; i.e., it is an empirical method to model average consumption of a fish population. The main advantages of Swenson's technique are that it is refined in comparison to other methods, and is not based solely on extrapolation of laboratory data (Mann 1978); i.e., it provides a fine scale diel feeding chronology from detailed site-specific environmental information and species-specific digestion rate relations.

Poe et al. (In Press) discuss the importance of the salmonid fishery resource in the Columbia River and the rationale for studying the predation rates of resident fish populations on juvenile salmonid smolts. Prior to this study, northern squawfish predation was generally believed to be an important cause of mortality to smolts in the Columbia River, especially when hatchery releases resulted in high prey abundances and in tailraces of dams (Thompson 1959; Ebel 1977). The main conclusion of a review on squawfish predation by Brown and Moyle (1981) was that squawfish do prey on salmonids in certain situations and are capable

Table 1. Scientific and common names of predator and prey fish species studied for consumption rate estimates in John Day Reservoir, Columbia River; and other fish species referenced in the text and tables.

Family	Species	Common Name
<u>Predator Species:</u>		
Cyprinidae	<u>Ptychocheilus oregonensis</u>	Northern squawfish¹
Percidae	<u>Stizostedion vitreum vitreum</u>	Walleye
Centrarchidae	<u>Micropterus dolomieu</u>	Smallmouth bass"
Ictaluridae	<u>Ictalurus punctatus</u>	Channel catfish
<u>Prey Species:</u>		
Salmonidae	<u>Oncorhynchus tshawytscha</u>	Chinook salmon
	<u>O. kisutch</u>	Coho salmon
	<u>O. nerka</u>	Sockeye salmon
	<u>Salmo gairdneri</u>	Steelhead
Cyprinidae	<u>Acrocheilus alutaceus</u>	Chiselmouth
	<u>Mylocheilus caurinus</u>	Peamouth
Catostomidae	<u>Catostomus columbianus</u>	Bridgelip sucker
	<u>C. macrocheilus</u>	Largescale sucker
Percopsidae	<u>Percopsis transmontana</u>	Sand roller
Cottidae	<u>Cottus beldingi</u>	Prickly sculpin
Clupeidae	<u>Alosa sapidissima</u>	American shad
<u>Other Species Referenced:</u>		
Cyprinidae	<u>Ptychocheilus grandis</u>	Sacramento squawfish
Percidae	<u>Perca fluviatilis</u>	Eurasian perch
	<u>P. flavescens</u>	Yellow perch
	<u>Stizostedion canadense</u>	Sauger
Centrarchidae	<u>Micropterus salmoides</u>	Largemouth bass
	<u>Lepomis macrochirus</u>	Bluegill
	<u>L. gibbosus</u>	Pumpkinseed
	<u>Pomoxis nigromaculatus</u>	Black crappie
Ictaluridae	<u>Ictalurus melas</u>	Black bullhead
	<u>I. nebulosus</u>	Brown bullhead

1. Juveniles of these species were also prey fish.

of consuming them in large numbers; however, they pointed out that more information is needed on squawfish bioenergetics and feeding, synecology, habitat requirements, factors causing predation dynamics, and the effects of dams on squawfish predation on salmonid smolts.

This work is the second in a series of four companion papers which together present the major findings of six-year fish predation research program conducted jointly by the U.S. Fish and Wildlife Service, and Oregon Department of Fish and Wildlife. In the first paper (Poe et al. In Press), qualitative diet analysis of the four main predators in the reservoir enables a conceptual food web model of species interactions within a lower Columbia River ecosystem to be developed. The primary purpose of this component of the research was to determine consumption rates by northern squawfish, walleyes, smallmouth bass, and channel catfish on seaward migrating Pacific salmon and steelhead in John Day Reservoir, with reference to environmental conditions which have been modified by the construction and management of the hydropower system. Quantification of predator-specific daily consumption rates presented in this paper and estimates of predator population size (Beamsderfer and Rieman In Press) are prerequisite to estimation of the numerical magnitude of predation and mortality rates of salmonid populations (Rieman et al. In Press).

For each of the four major fish predators, the specific study objectives were to: (1) determine the total daily ration of all food items, i.e. fish and non-fish. (2) determine mean monthly (April-August) daily consumption rates ($\text{prey} \cdot \text{predator}^{-1} \cdot \text{d}^{-1}$) on juvenile salmonids in McNary Dam tailrace restricted zone versus the remainder of John Day Reservoir for subsequent absolute loss estimates, (3) model overall trends of daily consumption rates of salmonid and non-salmonid prey fish on a temporal basis (five months), (4) model overall trends of daily consumption rates of salmonid and non-salmonid prey fish on a spatial basis (six reservoir areas), (5) model overall relations between predator size (age) and consumption rates of salmonid and non-salmonid prey fish and (6) determine the diel feeding chronology on salmonid and non-salmonid prey fish on a fine (2-h) time scale.

Methods

Study Design

A detailed description of the study site, characteristics of the salmonid smolt migration, predator collection methods, stomach contents analysis methods, and overall sampling design is presented by Vigg (1988) and Poe et al. (In Press). Predators were sampled on a diel

schedule (four 6-h periods per day) for at least three consecutive days during each month of the smolt out-migration (April-August) during 1983-1986; except in July, 1983 and July 1984. Four general reservoir regions sampled each year and their distance downstream from McNary Dam were: (1) McNary Dam tailrace, 5 km; (2) Irrigon, 20 km (3) Arlington, 75 km; and (4) John Day Dam forebay, 118 km. Regions (1) and (4) were subdivided into the area within one km of the dams (referred to here as restricted zones) and the remainder -- for a total of six reservoir areas. Arlington was not sampled in 1983; and the McNary Dam tailrace restricted zone (RZ) was the only area sampled each month in 1986.

For the purpose of subsequent absolute loss and mortality estimates (Rieman et al. In Press), consumption estimates were stratified by two reservoir areas: McNary Dam tailrace RZ and the remainder of the John Day Pool. Thus the a-priori hypothesis, developed by previous workers (e.g., Ebel 1977) that predation rates are higher immediately below Columbia River dams compared to other parts of the reservoir, could be tested.

For most consumption estimates, the data were pooled over the four years of study (1983-1986) for several reasons: (1) pooling resulted in a balanced study design, and larger sample sizes in the spatio-temporal strata of the consumption estimates; (2) the sampling design was unbalanced on a spatio-temporal basis during certain years (Poe et al. In Press); (3) diet composition of the predators was invariant among years (Poe et al. In Press); (4) numbers of hatchery-produced juvenile salmonids upstream from John Day Reservoir, and juvenile salmonid passage numbers at McNary Dam were relatively constant among years (Fish Passage Center 1987; Rieman et al. In Press); (5) predator population size was relatively constant among years (Beamesderfer and Rieman In Press); and, (6) environmental factors postulated to affect predation rates (e.g., temperature and flow) were relatively constant during the years of the study (U.S. Army Corps of Engineers, unpubl. data).

Consumption Estimation Technique

Consumption rate estimates were made for four predator species on two groups of prey fish: salmonids (four species) and non-salmonids (nine species) (Table 1). The technique we developed to estimate daily consumption rates was based on the original method of Swenson (1972); it involves eight steps (Figure 1): (1) stomach contents of predators are evaluated on a diel schedule throughout the period of juvenile salmonid migration; (2) original prey weight is predicted from body length and bone measurements; (3) percent digestion or mass evacuated is calculated from the difference between sample and original prey weights; (4) regression equations to predict evacuation rates as a function of time, temperature, fish size, and meal size are formulated from digestion experiments for each predator; (5) duration of the

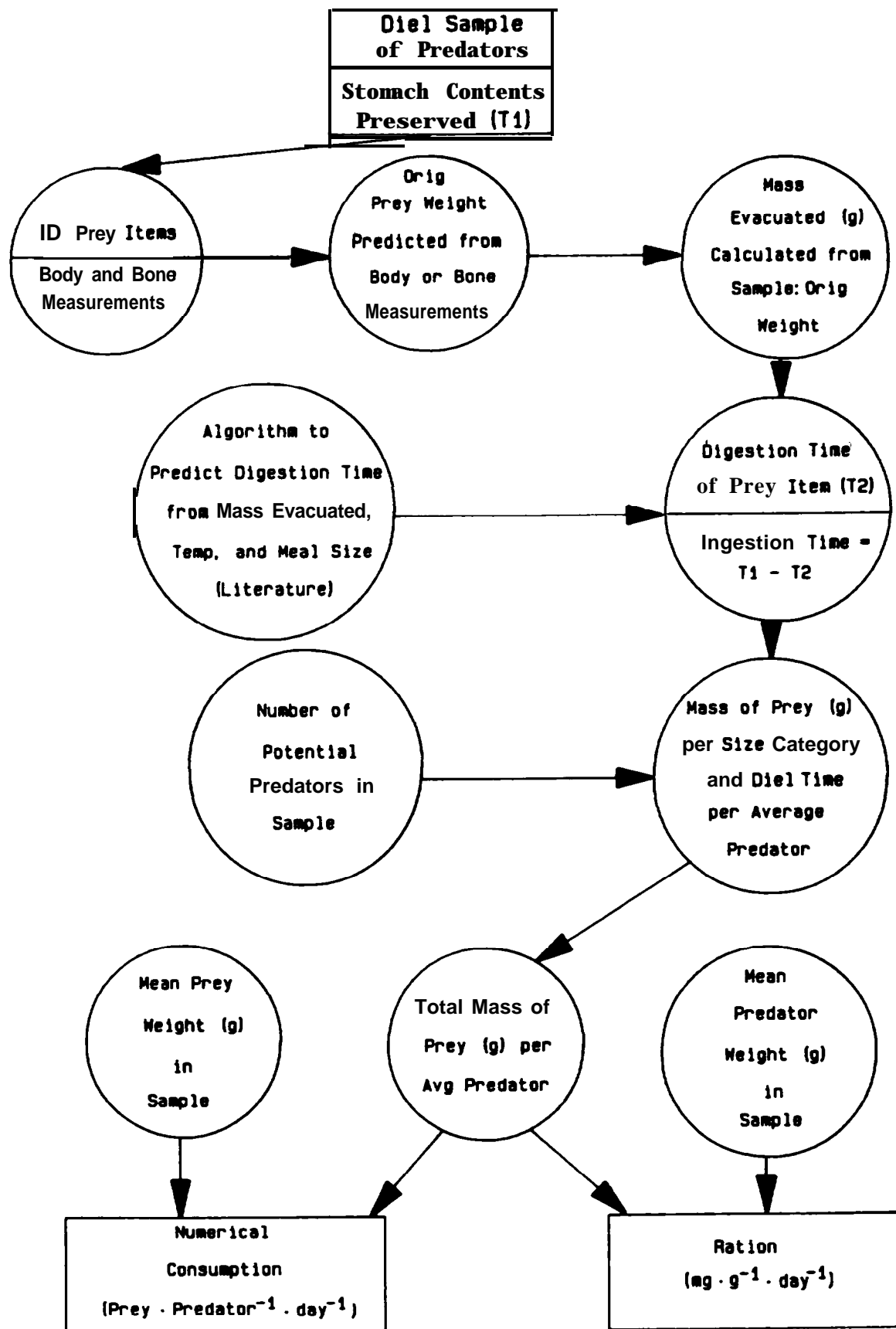


Figure 1. Flow Diagram showing the processes involved in calculating consumption rates using Swenson's technique.

digestion Period and time of ingestion of each Prey fish item are calculated from data derived from (3) and (4) above; (6) mass of Prey consumed Per diel time period Per prey size category Per day is calculated; (7) the data from (6) above are divided by the number of potential predators in the sample for each diel time-prey size strata -- to estimate mass consumed Per average predator; (8) daily ration ($m_{\text{prey}} \text{ g predator}^{-1} \text{ d}^{-1}$) and number of prey consumed ($\text{prey} \text{ predator}^{-1} \text{ d}^{-1}$) are derived from mean predator and prey weights for the sample. Thus, Swenson's technique reconstructs an average diel feeding pattern from pooled stomach contents of a sample of predators collected in situ. The consumption calculation can be summarized by the following equation:

$$C = \sum_{i=1}^t \sum_{j=1}^s \frac{\sum_{k=1}^p W_{ij}}{F_{ij}} \quad (1)$$

,where C is the daily consumption (g) of an average Predator, W_{ij} is the undigested weight of p Prey fish of a given size category (s), during a given diel time interval (t), and F_{ij} is the number of Potential predators from the sample which could-have contained prey fish of the given size (s) of a given digestion ($\leq 90\%$), during the given diel time Period.

Regression Equations

Swenson's technique requires the linkage of a series of regression equations to accomplish the various steps of the calculation procedure outlined above. Fork length was directly measured if Possible, however, for moderately digested Prey fish, various body length measurements were made depending on the fishes' condition; alternate body length measurements were converted to fork length using linear regression equations (Table 2). Hansel et al. (1988) present the prey species-specific regression equations to estimate prey fork length (mm) from various bone measurements -- for prey fish items of advanced digestion

Table 2. Linear regression model ($Y = a + bX$) statistics of fork Length (Y) regressed on other length measurements (X), solved by Least squares, for 11 species of prey fish in John Day Reservoir, Columbia River. Sample size for each prey fish is in parentheses.

Prey Species (n)	Nape to Tail			Standard			Total		
	a	b	R ²	a	b	R ²	a	b	R ²
American shad (44)	4.20	1.269	0.99	1.45	1.060	0.99	-0.15	0.890	0.99
Chinook salmon (53)	7.40	1.194	0.99	2.22	1.049	0.99	-2.16	0.941	0.99
Steelhead (46)	7.01	1.233	0.99	5.34	1.042	0.99	-1.57	0.958	0.99
Bridgelip sucker (52)	13.45	1.216	0.99	6.08	1.069	0.99	-3.94	0.961	0.99
Largescale sucker (58)	5.43	1.268	0.99	3.40	1.091	0.99	-1.64	0.936	0.99
Chinise lmouth (52)	8.40	1.217	0.99	4.01	1.077	0.99	-2.52	0.906	0.99
Peamouth (40)	-1.02	1.337	0.99	-1.80	1.144	0.99	-2.01	0.923	0.99
Northern squawfish (50)	5.60	1.299	0.99	1.81	1.083	0.99	-0.19	0.899	0.99
Sand roller (46)	2.45	1.373	0.94	2.16	1.094	0.96	0.90	1.890	0.96
Smallmouth bass (36)	7.61	1.172	0.99	1.85	1.101	0.99	0.01	0.956	0.99
Prickly sculpin (49)	2.18	1.458	0.99	3.44	1.151	0.99	0.00	1.000	1.00

for which body length measurements could not be made. Original prey fish weight was estimated from power model regressions on fork lengths (Table 3).

The mass of each prey fish evacuated was calculated as the difference between the estimated original weight of the item compared to its' digested weight; since the stomach contents were preserved in 10% formalin, a linear regression equation developed by Reyer et al. (1988) was used to estimate unpreserved digested weight from preserved weight. Time of digestion (h) for each prey item was estimated from predator species-specific evacuation rate regressions, solved for time (Table 4). Depending on predator species, digestion time was predicted from percent digestion or mass evacuated from the prey item, temperature, prey weight, predator weight, and/or meal size. Time of ingestion of each prey fish item was back-calculated from the time of predator capture and the prey item's duration of digestion.

Meal size, based on stomach contents of each individual predator, was calculated as a weight (g) for northern squawfish and smallmouth bass, or as a ration ($\text{mg } g^{-1}$) for walleye. Meal size weight (S, g) was calculated as the sum of: (1) the original weight of the specified prey fish item (O_i), (2) the original weights of any other prey fish items in the stomach that are within 10% of the original weight and 20% of the percent digestion of the specified prey item (O_j), and (3) the digested weight of all other food items in the stomach (\underline{Dk}):

$$S = O_i + O_j + Dk \quad (2)$$

Meal size ration (R, $\text{mg } g^{-1}$) was calculated as a proportion of meal size weight to predator weight (\underline{P} , g):

$$R = S \ 1000 / P \quad (3)$$

The total daily ration of all food items combined was determined from the gravimetric proportion of fish to non-fish food items in the diet (Table 5). Total ration (R_t) was calculated by extrapolation:

$$R_t = R_f / G \quad (4)$$

Where, R_f is the ration of prey fish, and G is the gravimetric fraction of fish in the diet.

Table 3. Power regression model ($Y = a \cdot X^b$) statistics of weight (Y, g) regressed on fork Length (X, mm), solved by least squares, for 11 species of prey fish in John Day Reservoir, Columbia River.

Prey Species	Sample Size (n)	Length Range (mm)	Regression Statistics		
			$a \cdot 10^{-6}$	b	R^2
American shad	40	39-98	4.600	3.106	0.99
Chinook salmon	148	34-184	16.943	3.031	0.98
Steelhead	122	93-206	8.395	3.003	0.89
Bridgelip sucker	52	89-214	5.321	3.161	0.99
Largescale sucker	58	61-229	6.531	3.131	0.99
Chiselmouth	52	99-242	22.080	2.907	0.99
Peamouth	40	57-194	9.638	3.038	0.99
Northern squawfish	50	40-238	12.677	2.970	0.99
Sand roller	46	30-110	16.943	2.984	0.96
Smallmouth bass	36	34-93	10.046	3.117	0.99
Prickly sculpin	49	40-137	5.309	3.187	0.99

Table 4. Algorithms for calculating predator-specific digestion times (h) based on evacuation rate regression equations for northern squawfish, smallmouth bass, walleye, & channel catfish.

predator Species	Algorithm to Solve for Digestion Time (h) ¹ .
Northern Squawfish ² .	$1330.753 E^{1.081} s^{-0.469} T^{-1.606} p^{-0.273}$
Smallmouth Bass ³ .	$268.529 (E + 0.01)^{0.696} s^{-0.364} e^{-0.139T} p^{-0.175}$
Walleye ⁴ .	<p><u>Prey: ≤ 1.1 g</u></p> $(-7.540 + 0.178 D + 0.088 R) / (0.0283 T^{1.1899})$ <p><u>Prey: $1.1-2.5$ g</u></p> $(-4.476 + 0.208 D + 0.031 R) / (0.0415 T^{1.1899})$ <p><u>Prey: > 2.5 g</u></p> $(-0.065 + 0.231 D + 0.047 R) / (0.0415 T^{1.1899})$
Channel Catfish ⁵ .	$0.327 D + .293 T$

1. Variable Definitions: E= prey mass evacuated (g)
S= prey meal weight (g)
R= prey meal ration ($mg \cdot g^{-1}$)
D= prey weight digested (%)
P= predator weight (g)
T= Temperature (C)
2. Beyer et al. (1988)
3. Beyer (Pers. Comm. 1986); Beyer and Burley (In press)
4. Swenson and Smith (1973); Wahl and Nielsen (1985)
5. Shrable et al. (1969)

Table 5. Proportion of the diets of four fish predators (northern squawfish, walleyes, smallmouth bass, and channel catfish) which is comprised of prey fish (percent by weight) versus non-fish food items, in John Day Reservoir, Columbia River, 1983-1986.

Predator Species/ Reservoir Area	Gravimetric Percentage of Fish in the Diet				
	April	May	June	July	August
-----v-----e-----					
<u>Northern squawfish</u>					
McNary Dam RZ:	92.5	97.8	84.0	96.6	86.2
John Day Pool:	79.1	74.3	43.4	44.8	49.3
<u>Walleyes</u>					
John Day Pool:	99.6	99.7	99.9	99.8	99.9
<u>Smallmouth Bass</u>					
John Day Pool:	85.1	81.8	76.7	92.2	82.9
<u>Channel Catfish</u>					
McNary Dam RZ:	72.9	95.3	88.0	98.0	
John Day Pool:	75.3	64.1	42.2	42.6	

Results

Total Daily Ration

Northern squawfish (over 250 mm in length) ate a higher mean proportion of fish in McNary RZ (91.4%) than in the John Day Pool (58%); as did channel catfish: 88.6 versus 56.1%. Smallmouth bass, greater than 200 mm in length, consumed an average of 81.7 percent fish; while walleyes of all sizes were almost exclusively piscivorous (99.8%). Northern squawfish and channel catfish showed similar temporal trends of total daily ration which were different from those of walleyes and smallmouth bass (Figure 2). In McNary Dam RZ, northern squawfish had the highest mean monthly total ration during July ($33.0 \text{ mg } \text{g}^{-1} \cdot \text{d}^{-1}$); likewise, channel catfish exhibited their highest ration during July-August ($16.7 \text{ mg } \text{g}^{-1} \cdot \text{d}^{-1}$). In John Day Pool, both predators showed a bimodal pattern with peaks in May and July; these peaks were about 17.5 and 25.5 $\text{mg } \text{g}^{-1} \cdot \text{d}^{-1}$ for northern squawfish and channel catfish, respectively. Walleyes exhibited an exponential increase in total ration from April to July (peak of $39.7 \text{ mg } \text{g}^{-1} \cdot \text{d}^{-1}$), with a subsequent decline in August. Smallmouth bass also had an exponential increase in total ration from April to July, but remained at the maximum ration of about $51.5 \text{ mg } \text{g}^{-1} \cdot \text{d}^{-1}$ during August.

The mean total ration over the entire season was remarkably consistent for all predators except smallmouth bass, which was about two times greater. Northern squawfish, channel catfish, and walleyes had total mean rations of 14.1, 12.6, and 14.2 $\text{mg } \text{g}^{-1} \cdot \text{d}^{-1}$, respectively. The mean seasonal total ration of smallmouth bass was $28.7 \text{ mg } \text{g}^{-1} \cdot \text{d}^{-1}$.

Consumption Estimates for Total Loss Calculation

Consumption estimates showed maximum predation rates on juvenile salmonids was by northern squawfish in the RZ during July (Table 6). Over the entire season, northern squawfish consumption of salmonids was over five times higher in the RZ versus the pool; i.e., a mean of 0.68 versus 0.13 $\text{prey } \text{predator}^{-1} \cdot \text{d}^{-1}$. Likewise, channel catfish had an order of magnitude higher mean seasonal consumption rates of juvenile salmonids in the RZ (0.50) than in the body of the reservoir (0.05 $\text{prey } \text{predator}^{-1} \cdot \text{d}^{-1}$). In the John Day Pool, walleyes exhibited the highest mean seasonal consumption rates on juvenile salmonids (0.19 $\text{prey } \text{predator}^{-1} \cdot \text{d}^{-1}$), which is similar in magnitude to that of northern squawfish. Of the predators studied, smallmouth bass had the lowest mean seasonal consumption rates on salmonids (0.04 $\text{prey } \text{predator}^{-1} \cdot \text{d}^{-1}$) in the reservoir. Insufficient numbers of walleyes and smallmouth bass were sampled in the RZ to make monthly consumption estimates.

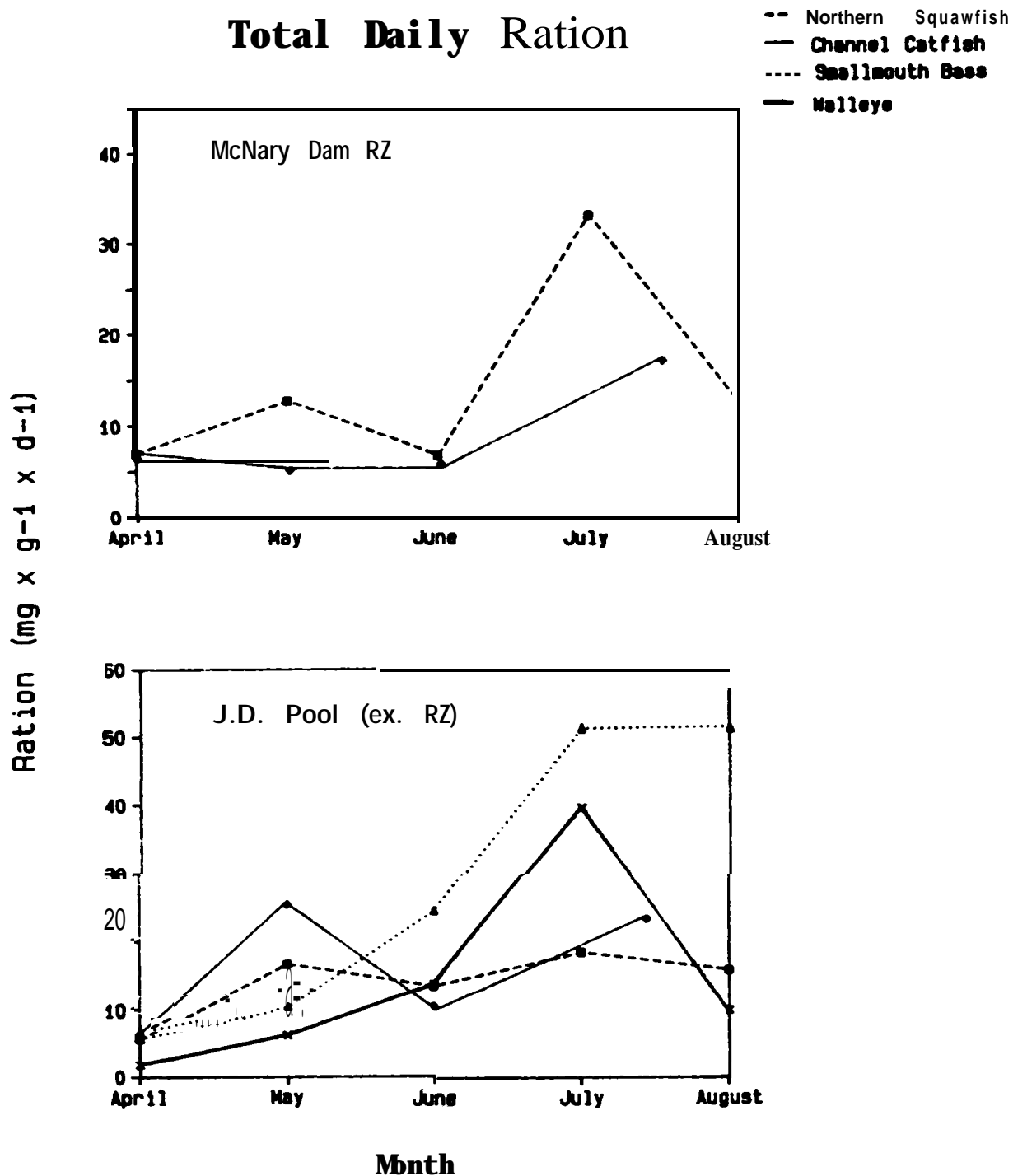


Figure 2. Mean monthly ration (fish + non-fish) of northern squawfish, walleyes, smallmouth bass, and channel catfish in McNary Dam restricted zone (RZ) and the remainder of John Day Reservoir (Pool), 1993-1986.

Table 6. Mean monthly consumption estimates (prey \times predator⁻¹ \times d⁻¹) of juvenile salmonids by four piscivores (northern squawfish, n= 4,377; walleye, n= 1,059; smallmouth bass, n= 2,880; and channel catfish, n= 656) in McNary Dam tailrace restricted zone (RZ) versus the remainder of John Day Pool, 1983-1986.

Predator Species ¹ (sample size)	Location	Salmonids per Predator per Day				
		April	May	June	July	August
Northern Squawfish						
(n= 2,371)	McNary RZ	0.139	0.490	0.358	2.027	0.392
(n= 1,996)	J.D. Pool	0.043	0.251	0.086	0.154	0.094
Walleye						
(n= 38)	McNary RZ	NP	NP	NP	NP	NP
(n= 1,021)	J.D. Pool	0.021	0.113	0.118	0.447	0.232
Smallmouth Bass						
(n= 24)	McNary RZ	NP	NP	NP	NP	NP
(n= 2,856)	J.D. Pool	0.003	0.009	0.019	0.118	0.070
Channel Catfish						
(n= 394)	McNary RZ	0.149	0.283	0.162	1.385	
(n= 262)	J.D. Pool	0.065	0.078	0.054	0.000	

1. Predator lengths: northern squawfish \geq 250 mm; walleye, all sizes; smallmouth bass \geq 200 mm; and channel catfish, all sizes.

NP= Predator not present in sufficient numbers to make monthly estimate.

Temporal Trends

Consumption rates of each predator varied on a monthly basis; the prey fish ration ($\text{mg prey} \cdot \text{g predator}^{-1} \cdot \text{d}^{-1}$) was generally lowest during April and highest during July (Figure 3). From April to August, the non-salmonid prey fish ration of northern squawfish increased from about 2.1 to 4.5 $\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ in McNary Dam RZ, and from about 1.0 to 3.0 $\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ in the reservoir. The salmonid component of the northern squawfish ration was relatively high in May and July at both reservoir areas; however, it peaked in the reservoir during May (9.7) and in the McNary Dam RZ during July (30.3 $\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$).

Channel catfish prey fish ration in the McNary Dam RZ was relatively constant from April to June (about 4.5 $\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$; but it tripled during the July-August period (16.3). In the John Day Pool, the fish ration of channel catfish was about 4.5 $\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ during both April and June, but increased in the May (16.7) and July-August (10.0) periods. In both reservoir areas, the proportion that salmonids comprised of the total fish ration of channel catfish decreased progressively from April to July-August; i.e., from 87 to 46% in the RZ, and from 29 to 0% in the John Day Pool.

The non-salmonid fish component of the ration of walleyes and smallmouth bass increased at an accelerating rate from April to July, reaching 35.1 and 39.9 $\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ for walleyes and smallmouth bass, respectively. During August, however, the non-salmonid fish component of walleyes ration decreased to 8.0 while that of smallmouth bass remained high, i.e., 40.6 $\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$. The salmonid component of walleyes' ration was maximum in July (4.6) and was relatively high during May and August (about 1.5 $\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) -- compared to the low salmonid consumption observed in April and June (< 0.4). Likewise, the salmonid component of smallmouth bass ration was highest in July and August (about 23 $\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$).

Spatial Trends

Mean daily numerical consumption rates of each predator, as well as the mean weight of predator populations and the prey fish they consumed, varied on a spatial basis within John Day Reservoir (Table 7). Mean daily salmonid and non-salmonid prey fish ration (which is a function of number of prey consumed, weight of prey, and weight of predator) showed different spatial trends for each predator species (Figure 4). Northern squawfish exhibited a high ration of salmonids at McNary Dam RZ (11.3 $\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$), relatively low rations (< 4.3) throughout the main body of the John Day Pool, and increased ration (> 6.5) at John Day Dam RZ and forebay. The non-salmonid component of northern squawfish ration, however, was lowest at McNary Dam RZ, relatively high throughout the reservoir, and highest at John Day Dam RZ.

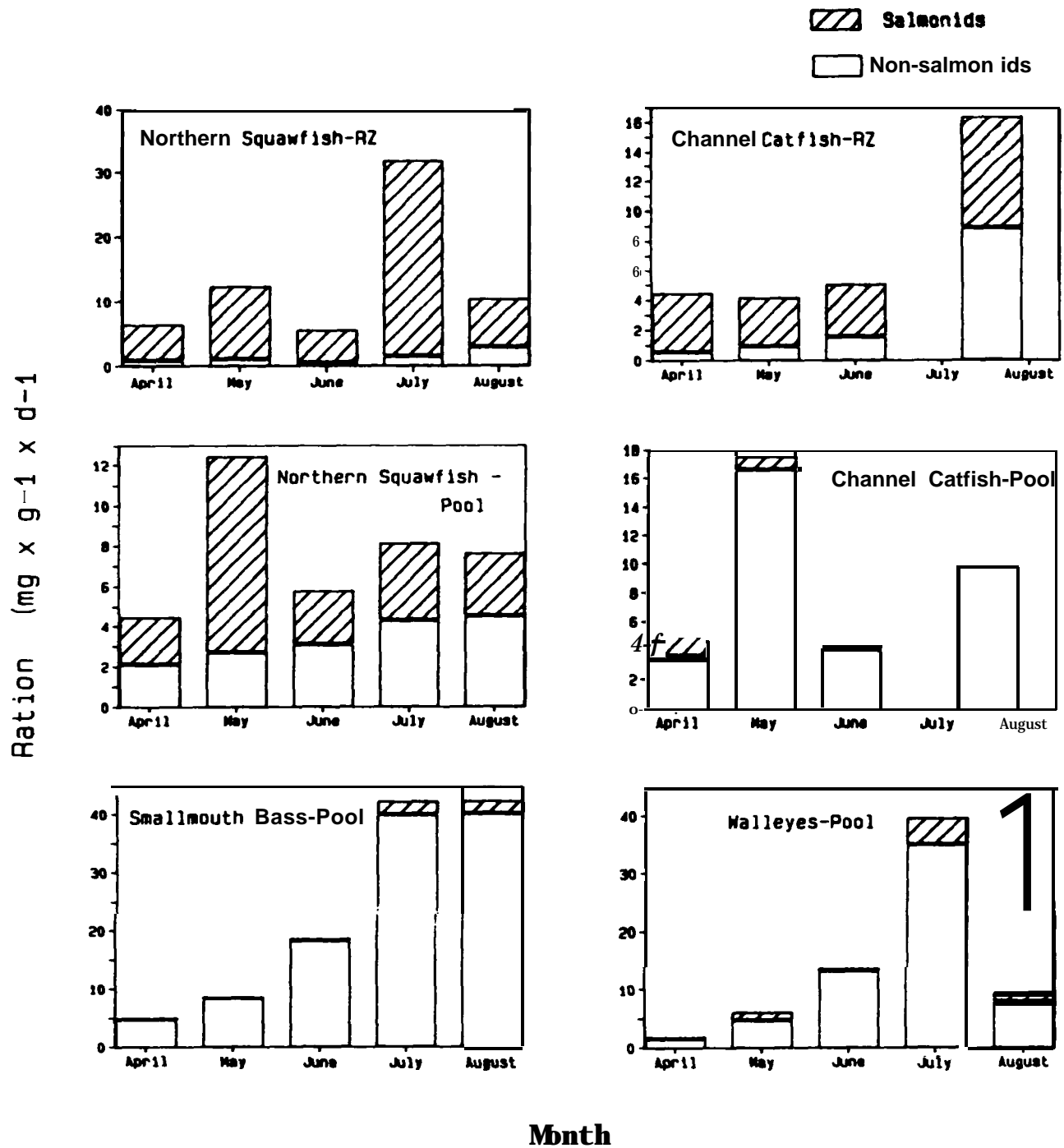


Figure 3. Mean monthly consumption rates of northern squawfish, walleyes, smallmouth bass, and channel catfish on salmonid and non-salmonid prey fish in McNary Dam restricted zone (RZ) and the remainder of John Day Reservoir (Pool), 1983-1986.

Table 7. Mean daily consumption rates ($\text{prey} \cdot \text{predator}^{-1} \cdot \text{d}^{-1}$) of northern squawfish, walleyes, smallmouth bass, and channel catfish on salmonid and non-salmonid preyfish in six areas of John Day Reservoir, 1983-1986. The six areas and their distance (km) downstream from McNary Dam are: McNary Dam RZ, 1; McNary Tailrace, 5; Irrigon, 20; Arlington, 75; John Day Forebay, 119; John Day Dam RZ, 123.

Predator Species:		Station, distance (km) from McNary					
Prey Group	Statistic ¹	-----					
		1	5	20	75	118	123
<u>Northern squawfish:</u>							
	n	2373	414	236	448	497	409
	W	997	854	802	737	685	783
Salmonid:	C	0.605	0.146	0.028	0.053	0.138	0.236
	W	18.5	24.7	26.8	31.6	32.6	33.6
Non-salmonid:	C	0.094	0.331	0.181	0.180	0.206	0.357
	W	12.6	20.4	21.4	23.8	27.6	25.1
<u>Walleye:</u>							
	n	38	659	338	27	0	0
	W	3109	2149	2505	1135	-	-
Salmonid:	C	0.000	0.072	0.144	0.745	-	-
	W		20.9	16.3	13.0	-	-
Non-salmonid:	C	0.529	0.676	1.128	1.320	-	-
	W	27.0	18.4	21.9	15.5	-	-
<u>Smallmouth bass:</u>							
	n	24	166	1033	836	635	192
	W	517	515	544	462	292	225
Salmonid:	C	0.051	0.014	0.052	0.023	0.011	0.083
	W	0.3	16.4	3.7	6.2	16.7	13.3
Non-salmonid:	C	0.358	1.428	0.927	0.652	0.473	0.321
	W	5.0	8.5	9.6	10.8	15.4	10.2
<u>Channel catfish:</u>							
	n	394	59	149	52	2	0
	W	2111	1606	1957	931	-	-
Salmonid:	C	0.239	0.048	0.053	0.000	-	-
	W	32.4	10.1	26.2	-	-	-
Non-salmonid:	C	0.130	0.531	0.549	0.197	-	-
	W	21.1	20.9	39.7	14.9	-	-

1. Definition of symbols representing statistics:
n = number of predators
W = Mean weight (g) of predators or prey
C = mean daily numerical consumption rate ($\text{prey} \cdot \text{predator}^{-1} \cdot \text{day}^{-1}$) of predators on prey fish.

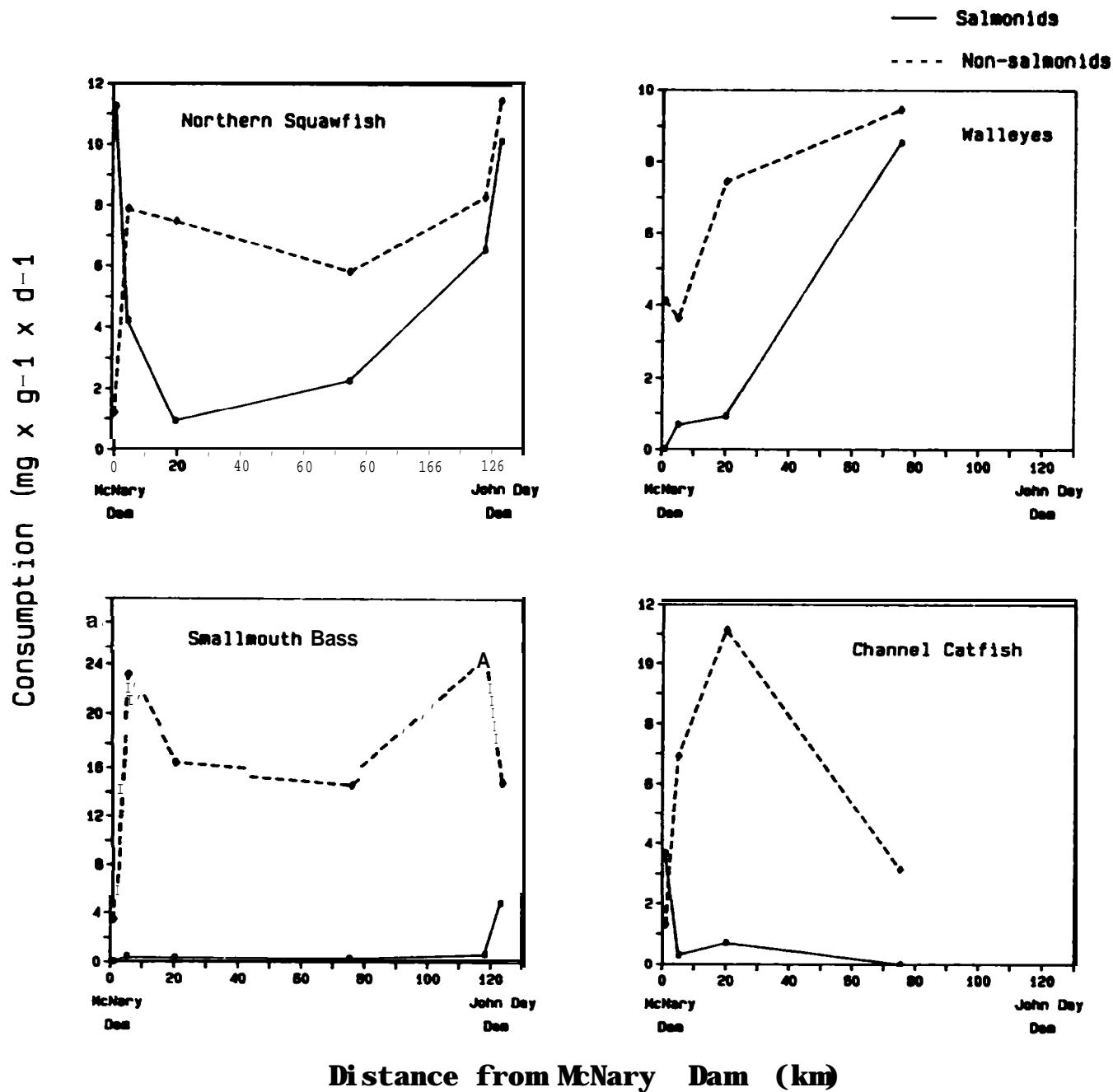


Figure 4. Mean areal consumption rates of northern squawfish, walleyes, smallmouth bass, and channel catfish on salmonid and non-salmonid prey fish in six sampling stations in John Day Reservoir, 1983-1986. The six areas are 1, 5, 20, 75, 118, and 123 km downstream from McNary Dam.

The spatial trend of channel catfish consumption resembled that of northern squawfish, except that channel catfish were not captured (and thus assumed to be rare) in the John Day forebay and RZ. Peak ration of salmonids occurred at McNary Dam RZ ($3.7 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$), while the highest consumption of non-salmonids (11.8) occurred at Irrigon, about 20 km downstream. Walleyes' spatial consumption pattern, unlike that of northern squawfish, showed a very low ration ($< 1.0 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) of salmonids in the upper 20 km of the reservoir (McNary Dam to Irrigon), but high ration 75 km downstream at Arlington (8.5). Similarly, the consumption of non-salmonids progressively increased from $4.1 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ at McNary Dam RZ and tailrace, to 9.5 at Arlington. We did not capture any walleyes with extensive sampling at John Day Dam RZ and forebay -- and therefore must assume that since they are rare, walleye predation is negligible in this region. Smallmouth bass had a very low consumption rate of salmonids throughout the reservoir ($< 0.5 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$), with the exception of an elevated ration (4.9) at John Day Dam RZ. Conversely, their ration of non-salmonids was high ($> 15.3 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) throughout the reservoir, with the exception of relatively low rates (3.4) at McNary Dam.

Predator Size (Age) Relations

Each predator showed trends in consumption rates with changes in size category; approximate fish size (fork length, mm; weight, g) to age relationships are presented in Table 8. Age structures of the predator populations were presented by: Rieman and Beamesderfer (In Press), for northern squawfish; Connolly and Rieman (In Press) for walleye and smallmouth bass; and approximated for channel catfish by Bennett et al. (1983). Overall prey fish consumption by northern squawfish progressively increased with size and corresponding age (Figure 5.). Numerical consumption and ration leveled off at about $0.8 \text{ prey} \cdot \text{predator}^{-1} \cdot \text{d}^{-1}$ and $14.0 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ for northern squawfish over 12 years of age. As the predator grew, salmonids composed an increasing proportion of the total prey fish ration -- over 75 percent for northern squawfish over 8 years old. Mean weight of prey fish consumed was directly related to northern squawfish age; non-salmonid prey fish were slightly larger than salmonids consumed, except for predators age 13 and above.

Channel catfish showed a pattern similar to that of northern squawfish; i.e., both total prey fish ration and the salmonid component increased with age (Figure 6). The highest prey fish ration ($16.0 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) was exhibited by channel catfish 431-465 mm in length (approximately seven years old). The prey fish consumption of channel catfish less than 466 mm in length (8 years) consisted mostly of non-salmonids; whereas those 466-673 mm (8-14 years) had a fish ration of about 50% salmonids, and those 674 mm (15 years) and above consumed only salmonids. Mean weight of fish consumed by channel catfish generally increased with predator size, but was variable.

Table 8. Approximate size ranges (fork length, mm) corresponding to ages (years) of northern squawfish, walleyes, smallmouth bass, and channel catfish from John Day Reservoir, Columbia River. Mean weight (g) of predators from consumption data files, by length intervals, are in parentheses.

Age (years)	Fork Length (mm) and		Weight (g) by Species	
	Northern squawfish ¹	Walleyes ²	Smallmouth bass ²	Channel catfish ³
0	1-34 (1)	1-109 (-)	1-45 (-)	1-26 (-)
	35-101 (4)	110-299 (179)	46-127 (20)	27-88 (-)
2	102-166 (35)	300-428 (653)	128-201 (76)	89-166 (-)
3	167-220 (88)	427-505 (1342)	202-265 (201)	167-246 (137)
4	221-263 (174)	506-557 (1878)	266-314 (409)	247-316 (414)
5	264-298 (259)	558-597 (2371)	315-353 (646)	317-379 (649)
6	299-327 (378)	598-630 (2797)	354-385 (913)	380-430 (1022)
7	328-354 (499)	631-653 (3390)	386-409 (1155)	431-465 (1331)
8 ⁴	355-379 (626)	654-670 (3579)	410-432 (1329)	466-494 (1671)
9	380-402 (779)	671-695 (4014)	433-452 (1626)	466-494 (1671)
10	403-423 (955)	696-718 (4389)	453-466 (1815)	466-494 (1671)
11	424-441 (1071)	>= 719 (5375)	>= 467 (1929)	466-494 (1671)
125	442-458 (1226)			495-589 (2310)
13	459-477 (1352)			495-589 (2310)

Table 8. (continued)

14	478-493 (1498)	590-673 (37451)
15	>= 494 (1653)	>= 674 (4008)

- 1 Age-length data from Rieman and Beamesderfer (In Press)
- 2 Age-length data from Connolly and Rieman (In Press)
- 3 Age-length data from Bennett et al. (1983)
- 4 Channel catfish ages 8 to 11 are combined.
- 5 Channel catfish ages 12 and 13 are combined.

Northern Squawfish

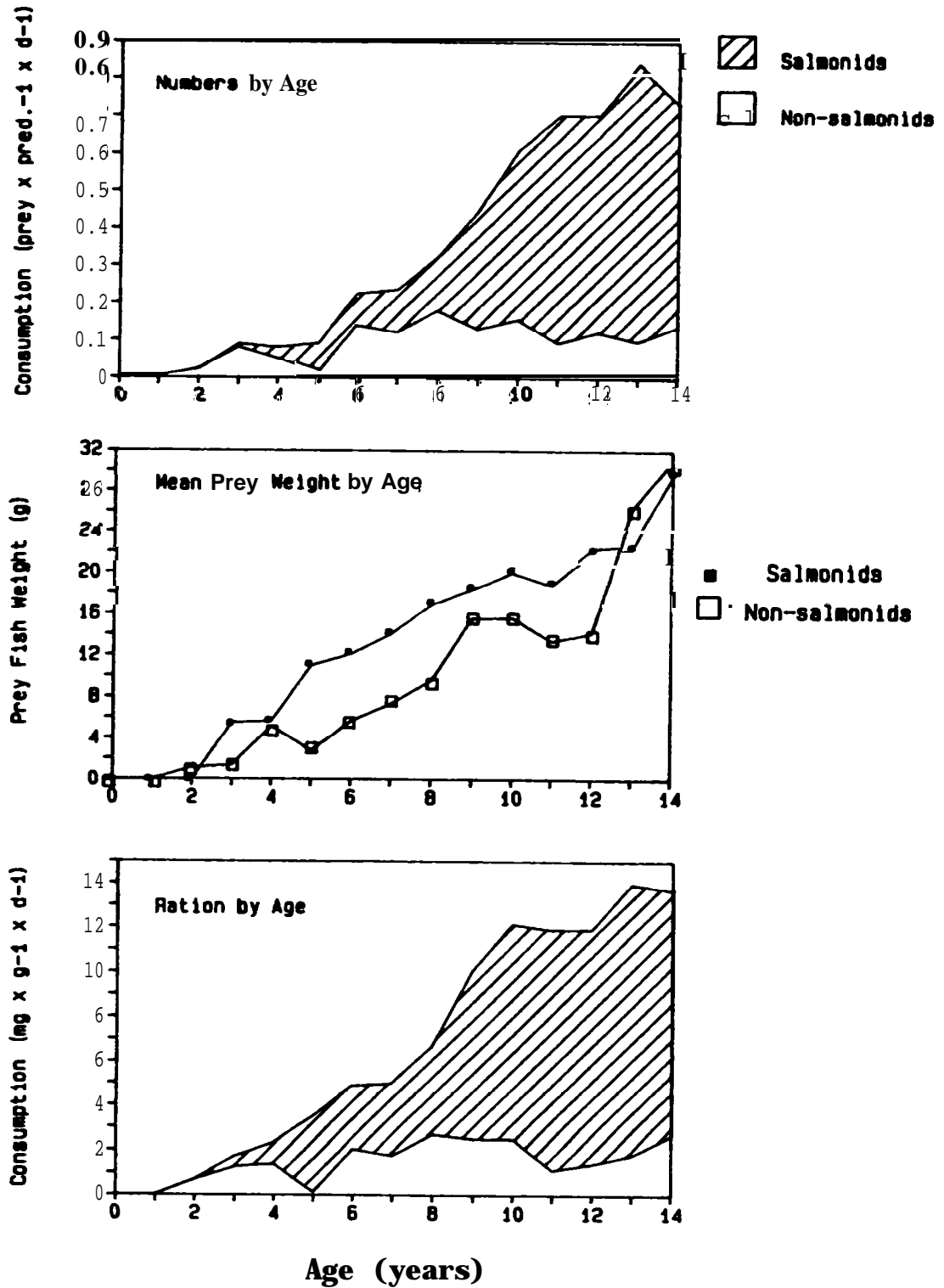


Figure 5. Mean age-specific consumption rates of northern squawfish on salmonid and non-salmonid prey in John Day Reservoir (all locations), 1983-1986.

Channel Catfish

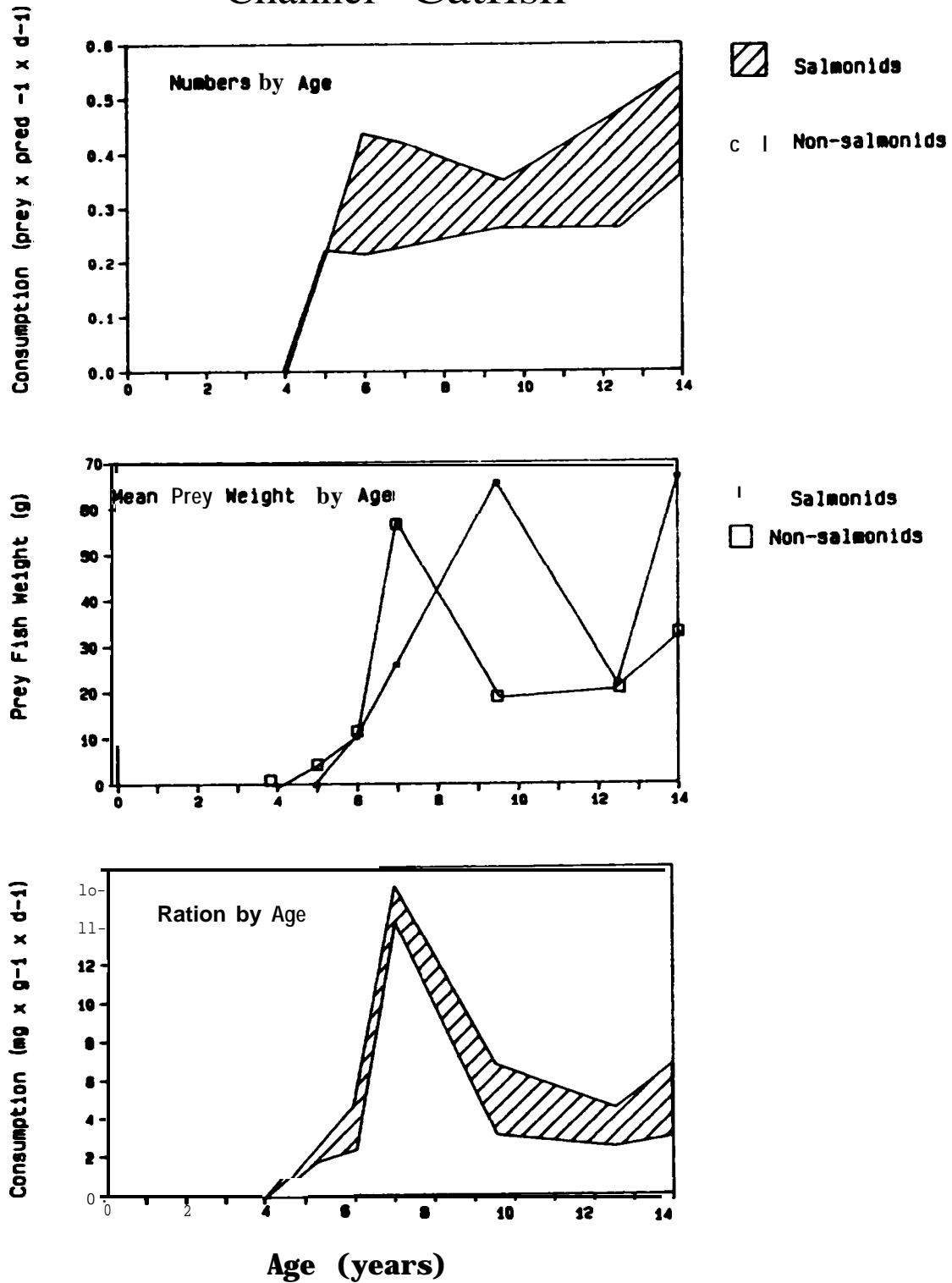


Figure 6. Mean age-specific consumption rates of channel catfish on salmonid and non-salmonid prey in John Day Reservoir (all locations), 1983-1986.

Walleyes and smallmouth bass were similar to each other in age-specific consumption trends, but differed markedly from northern squawfish and channel catfish. Walleye numerical consumption rate of prey fish peaked at two years of age ($1.0 \text{ prey } \text{predator}^{-1} \text{ d}^{-1}$), followed by a slight decline and leveling off at about 0.8 fish per day (Figure 7). The corresponding ration showed a more pronounced peak ($38.8 \text{ mg } \text{g}^{-1} \text{ d}^{-1}$) at one year of age and subsequent decline to about 6.5 for walleye older than two years. The proportion of walleyes' ration comprised of salmonids decreased with age: from about 30% at two years to about one percent at eight years; older walleye in our sample did not eat salmonids. Mean weight of salmonids eaten by walleyes over three years old was relatively constant, whereas weight of non-salmonid prey fish continued to increase with predator size over the entire range. Smallmouth bass also exhibited highest prey fish ration at two years of age ($25.2 \text{ mg } \text{g}^{-1} \text{ d}^{-1}$), followed by subsequent declines (Figure 8). Numerical consumption was also high at 2-4 years of age ($0.75 \text{ prey } \text{predator}^{-1} \text{ d}^{-1}$) followed a slight increasing trend for older fish. The salmonid component of smallmouth bass consumption ranged from about 1 to 7% for ages 1 to 6; no salmonids were consumed by older smallmouth bass. Mean salmonid prey weight ranged about 5 to 10 g for smallmouth bass 2 to 6 years of age; non-salmonid prey fish generally increased with smallmouth bass size (and corresponding age) but showed a decelerating rate of increase for fish over three years old.

Diel Feeding Chronology

Consumption rates varied, for each predator, according to time of day. These diel patterns were generally consistent throughout the season. Increased feeding activity of northern squawfish in John Day Pool commenced at dawn and extended to the afternoon (0400-1600 hours); diel feeding chronology in McNary Dam RZ was bimodal with a nocturnal peak (2400-0400), and another after sunrise at 0600-1000 hours (Figure 9). In McNary Dam RZ, northern squawfish fed almost entirely on juvenile salmonids; but in the rest of the reservoir, squawfish fed on almost equal numbers of salmonids and non-salmonids and the feeding periodicity was similar for both types of prey.

The other three predators generally had a bimodal diel feeding pattern, but it varied by species (Figure 10). Walleyes fed primarily during the day from 0800 to 1600 hours, but also fed actively at night with two sharp peaks occurring at 2200 to 2400 hours and 0200 to 0400 hours. There was no obvious diel trend in the amount of salmonids consumed by walleye. However, the proportion of salmonids consumed was greatest during 0400-0800 hours and least during 1800-2000 hours. Feeding by smallmouth bass occurred throughout the diel cycle. Feeding activity was lowest during the night (2200-0600), increased from 0600 to 1400 hours, was relatively low from 1400 to 2000 hours, and exhibited

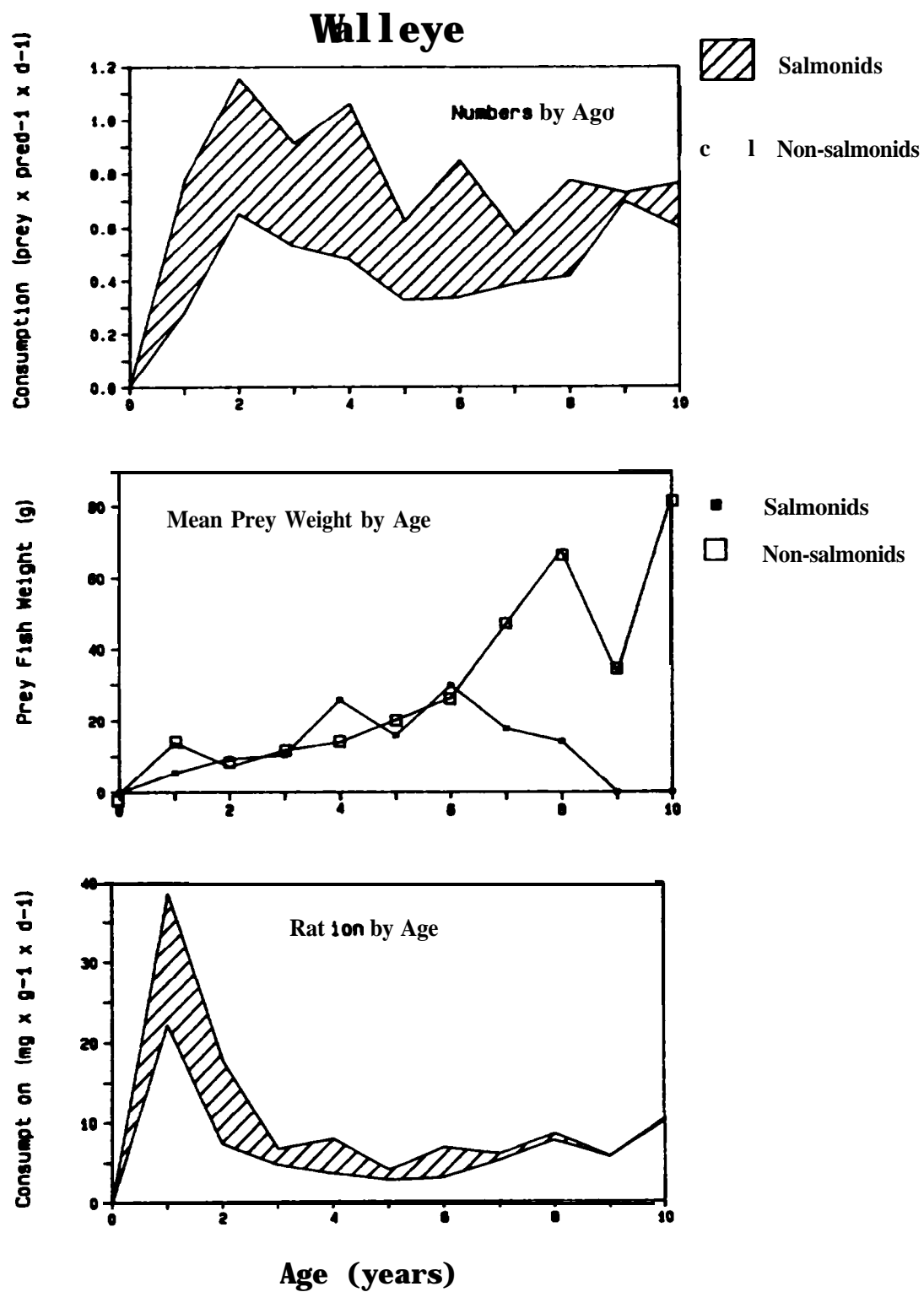


Figure 7. Mean age-specific consumption rates of walleyes on salmonid and non-salmonid prey in John Day Reservoir (except McNary Dam restricted zone), 1983-1986.

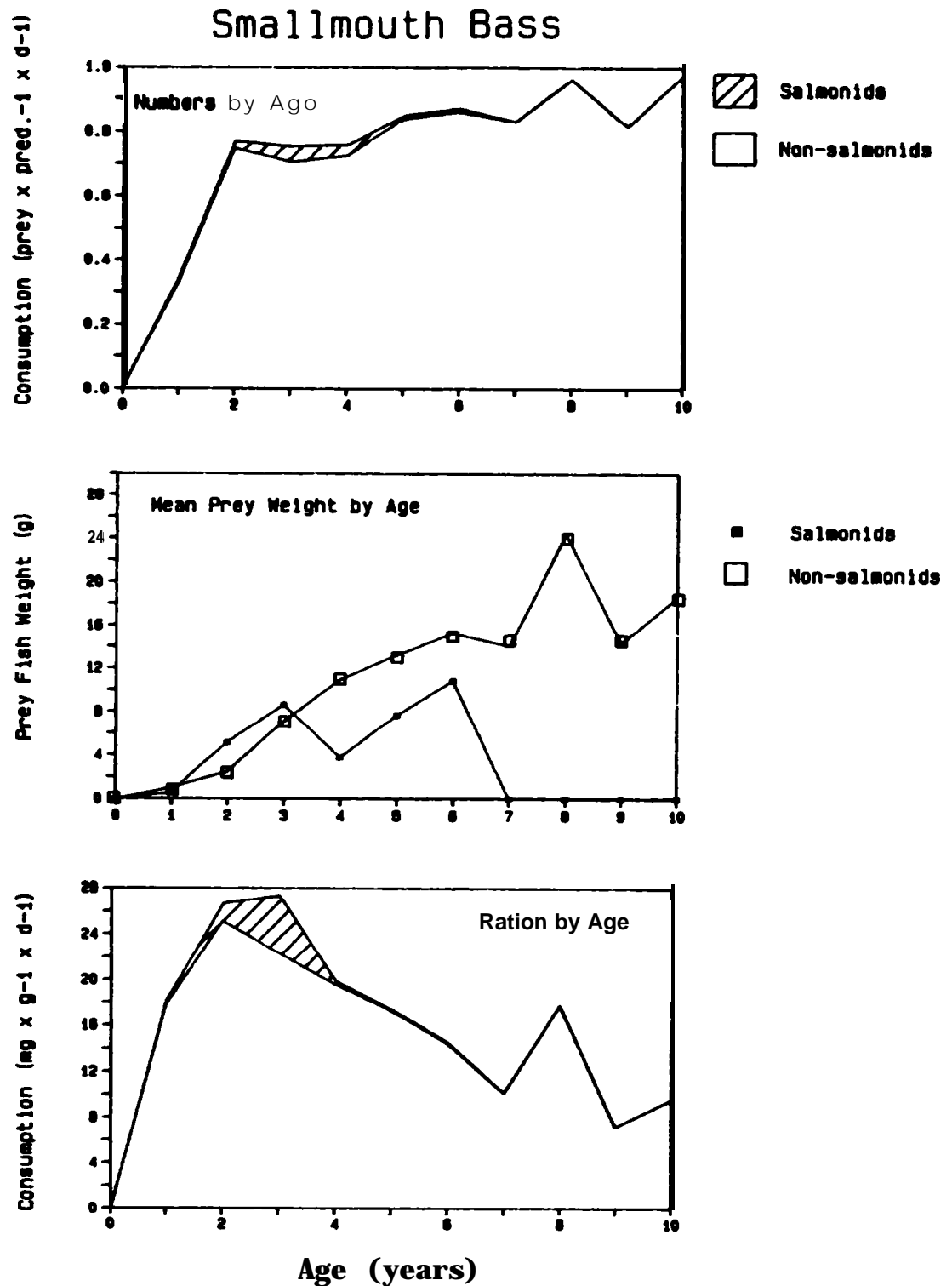


Figure 8, Mean age-specific consumption rates of smallmouth bass on salmonid and non-salmonid prey in John Day Reservoir (except McNary Dam restricted zone), 1983-1986.

Northern Squawfish

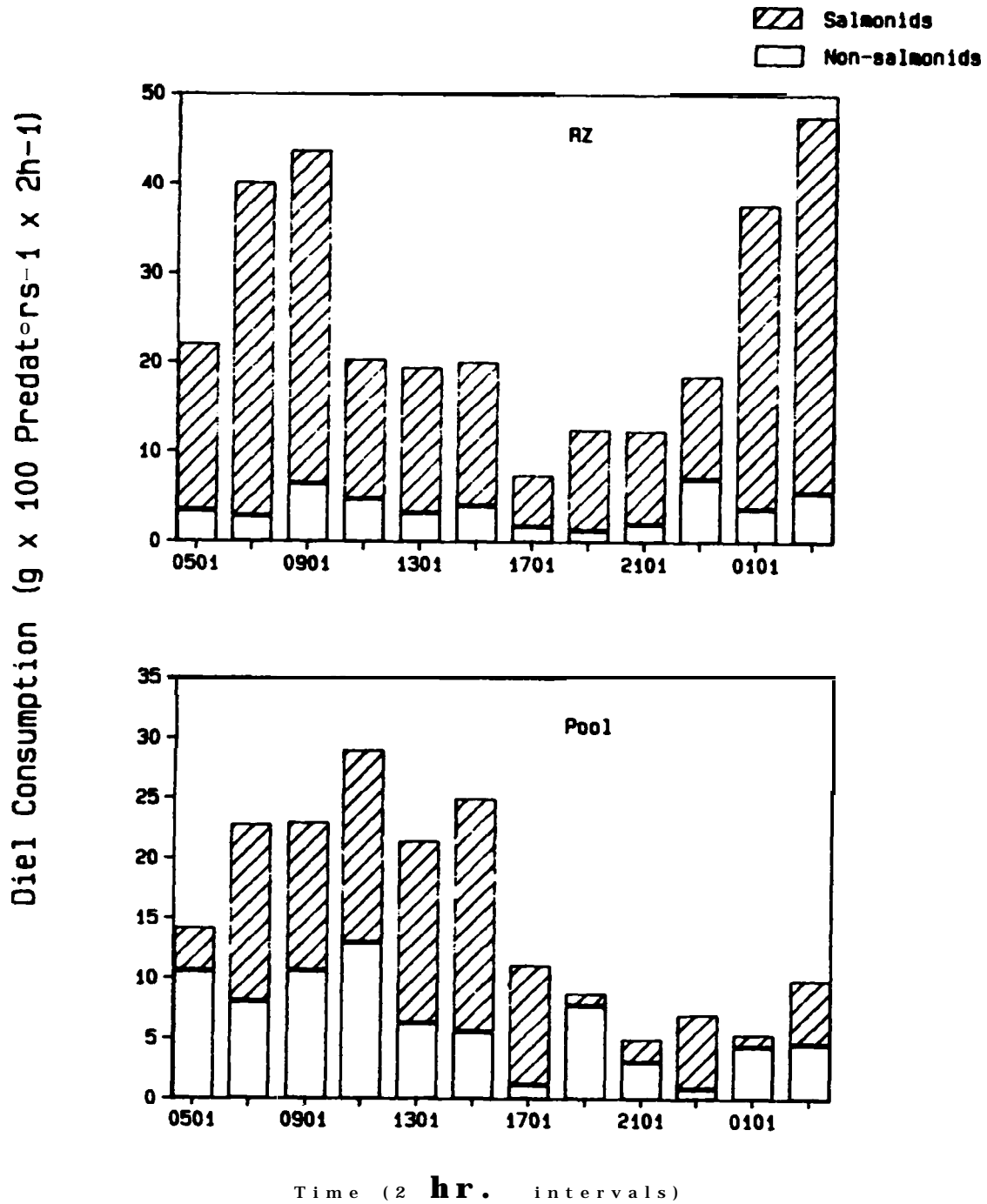


Figure 9. Diel consumption rates ($g \cdot 100 \text{ predators}^{-1} \cdot 2 \text{ h}^{-1}$) of northern squawfish on salmonid and non-salmonid prey fish in McMary Dam restricted zone (RZ) and the remainder of John Day Reservoir (Pool), 1983-1986.

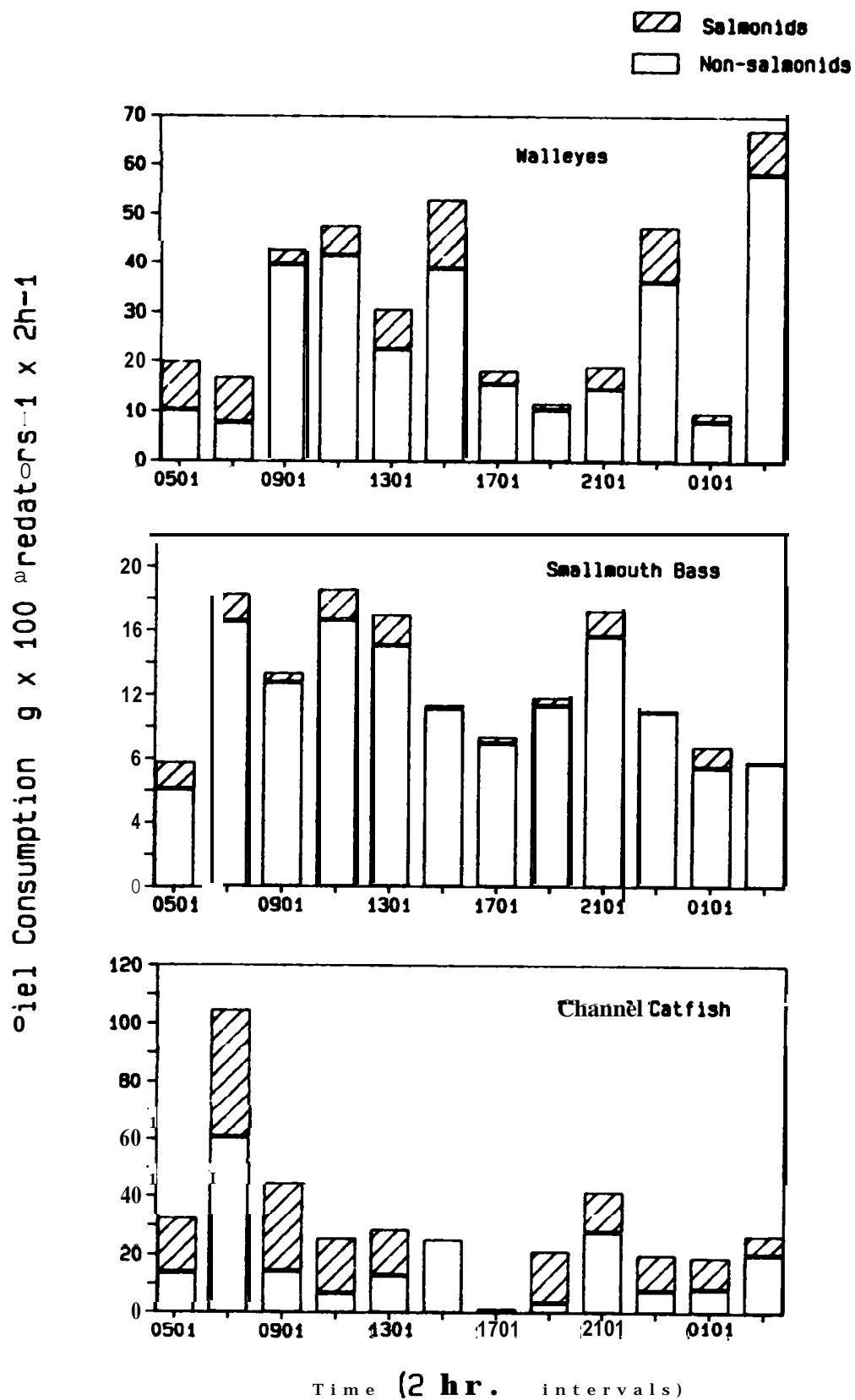


Figure 10. Diel consumption rates ($\text{g} \cdot 100 \text{ predators}^{-1} \cdot 2 \text{ h}^{-1}$) of walleyes, smallmouth bass, and channel catfish on salmonid and non-salmonid prey fish in John Day Reservoir, 1983-1986.

a peak near sunset (2000 to 2200 hours). Channel catfish exhibited a bimodal crepuscular feeding pattern with a peak feeding activity occurring near sunrise and sunset. No diurnal preference for salmonid versus non-salmonid prey was apparent; e.g., no one predator fed mostly on salmonids at night and switched to mostly non-salmonids during the day.

Discussion

Food consumption by fish in nature is not a simple, uniform phenomenon -- homogeneous with respect to characteristics of the predator and its environment. Instead, predation is dynamic -- the observed level is a function of many complex biotic and abiotic factors. We modeled consumption rates as a function of predator size, month, reservoir area, and diel time period in order to illustrate important aspects of the dynamics of predation. In the following sections, the observed patterns of consumption by four piscivores in John Day Reservoir are interpreted in terms of the biology of the species and the conditions of the environment. An understanding of the theoretical bases of the observed dynamics of consumption will increase our capacity to generalize the ecological mechanisms involved in the predator-prey relations in John Day Reservoir.

Many factors affected spatio-temporal trends in consumption rates of fish predators in John Day Reservoir, including: metabolic requirements, distribution, feeding behavior, spawning, and prey availability. These biological factors are controlled to some extent by the genetics of the species, but are certainly mediated by the environment. Metabolism of poikilotherms is greatly affected by temperature, which varies in a predictable seasonal way. Feeding activity, in turn, is a function of metabolic requirements, as well as other variables such as food availability. In a similar fashion, spawning is triggered by seasonal cues including temperature. However, under natural conditions it is difficult to decompose a seasonal factor and differentiate the effects of temperature from other variables such as photoperiod and water flow. Food availability in John Day Reservoir has a baseline invertebrate and resident fish component, and a highly seasonal salmonid migration component. The empirical relation between salmonid prey density and northern squawfish predation rates in McNary Dam tailrace was described by Vigg (1988). Prey selectivity relations in John Day Reservoir were reported by Poe et al. (In Press).

Temperature Relations

Temperature has a multiple role which pervades every aspect of fish ecology (Fry 1947); the combined information concerning lethal levels and levels for optimal physiological performance, at all stages of development, is necessary to interpret the overall effect of temperature (Brett 1956). Temperature plays a highly regulatory role in fish physiology: it controls reproductive cycles, the rate of digestion, the rate of respiration, and bio-chemical activities within a fish (Mount 1969). Thus, temperature is probably the most influential single variable regulating consumption rates of fish in nature.

Little is known about the thermal relations of northern squawfish; the upper lethal temperature range of northern squawfish acclimatized at 18.9-22.2°C was: 26.4, 29.3, and 32.0°C for 0, 50, and 100% mortality, respectively (Black 1953). The preferred temperature range of Sacramento squawfish in a California stream varied by month, with the maximum preferred temperature in July (mean \pm SD): 16.8 \pm 1.7 to 20.1 \pm 1.7°C (Baltz et al. 1987). Digestion rate of northern squawfish increases with temperature over the range of about 5 to 28°C (Falter 1969; Steigenberger and Larkin 1974; Beyer et al. 1988). Likewise, given an unrestricted food supply, maximum consumption rate increases exponentially to some optimum temperature and subsequently declines to zero consumption just below the incipient lethal level (Vigg and Burley In Preparation). Patten and Rodman (1969) observed northern squawfish spawning at temperatures of about 17°C in a Lewis River reservoir. In John Day Reservoir, temperature ranged about 15-19°C during the period of peak spawning (Vigg and Prendergast In Preparation). In McNary Dam RZ, juvenile salmonid density is an important determinant of consumption rates of northern squawfish; and smolt passage through McNary Dam was bimodal during 1983-1986, with peaks in May and July (Vigg 1988). Temporal consumption rate in McNary Dam RZ was also bimodal, however, the mean rate in July (2.0 prey, predator⁻¹, d⁻¹) at 19.0°C was four times that in May (0.5 prey, predator⁻¹, d⁻¹) at a mean temperature of about 11.5°C.

Walleye prefer temperatures of 21-23°C, which is within the range for optimum growth (20-25°C); their physiological optimum is 22.6°C, and their upper incipient lethal level is 31.6°C (Koenst and Smith 1975; Hokanson 1977). Maintenance ration showed an exponential relationship with temperature, over the 4 to 20°C range (Ware 1972). This observation is consistent with the exponential increase in walleye daily ration exhibited in John Day Reservoir from April to July (Figure 2).

Optimum physiological temperatures for smallmouth bass are substantially higher than those of northern squawfish and walleye; i.e., preferred temperatures were reported as 28.0°C in the laboratory and 20.3-21.3°C in temperate natural habitats (Ferguson 1958). Depending on seasonal acclimatization, final preferendum of smallmouth bass was 18-31°C for young of the year, and 12-30°C for adults (Barans and Tubb

1973; Reutter and Herdendorf 1974). Stauffer et al. (1976) calculated a final temperature preference of 30.8°C in the laboratory, but preferred habitat in the field was apparently related more to forage fish movements than temperature. Growth rates in the laboratory for both largemouth and smallmouth bass appear optimal between 25 to 29°C (Coutant 1975; Shutter et al. 1985; Coutant and DeAngelis 1983). Maximum daily ration of largemouth bass increases with temperature to an optimum (27.5°C) and then declines to zero at 37.0°C (Niimi and Beamish 1974; Rice et al. 1983). The temporal consumption rates of smallmouth bass (Figure 2) show an exponential increase from April to July, and leveling off in August; this trend suggests the August thermal regime may be optimal for smallmouth bass consumption in John Day Reservoir.

Channel catfish, given a wide range of temperatures, prefer temperatures of 33.8°C (experimental) to 33.9-35.0°C (field) (Stauffer et al. 1976). Feeding experiments indicated that channel catfish digestion rates were directly related to temperature, and were high at 21.1 to 29.4°C (Shrable et al. 1969). Channel catfish food consumption and conversion efficiency was highest above about 26.5°C and 14 h day lengths (Kilambi et al. 1971). Similarly, West (1966) observed maximum conversion efficiency at 28.9°C and maximum growth at 29-30°C. In aquaculture of channel catfish, food conversion and consumption are low at temperatures less than 16-18°C (Andrews and Stickney 1972). Channel catfish foraging activity, as indicated by angler catch/effort, was directly related to water temperature in a Missouri lake ($r = 0.9$); and was highest in July at the maximum temperature of about 27°C (Eder and McDannold 1987). In aquaculture ponds, channel catfish did not begin feeding until water reached 12°C and did not feed on a daily basis until water temperature reached 22°C (Randolf and Clemens 1976). Thus the optimum temperature for channel catfish consumption is the highest of any piscivore in John Day Reservoir; and highest consumption rates would be expected in August. The temporal trend in McNary Dam RZ shows a relatively constant ration from April to June, with more than triple the ration during July-August (Figure 2). Prey availability may be limiting in the John Day Pool, however, since peak consumption occurs during both May and July-August -- corresponding to juvenile salmonid passage.

The maximum daily water temperature flowing through McNary Dam (22°C) usually occurs in August (U.S. Army Corps of Engineers, unpubl. data); corresponding sub-surface maximum temperatures in shallows and backwaters of John Day Reservoir are about 26°C (U.S. Fish and Wildlife Service, unpubl. data). Thus, the highest water temperatures occurring in John Day Reservoir are at or below the thermal preference and optimum temperature for consumption and growth of all predators except northern squawfish; i.e., the thermal range gives northern squawfish a greater opportunity to select their physiological optimum habitat.

Spawning Relations

Spawning activity may depress consumption rates during the species-specific season. Peak spawning of northern squawfish in John Day Reservoir occurs in June (Viqq and Prendergast In Preparation); our results show lower consumption rates and a higher percentage of empty stomachs during this month. Furthermore, the functional response of northern squawfish consumption to prey density breaks down in June (Viqq 1988). Steigenberger and Larkin (1974) found only trace amounts of food in a sample of 85 spawning northern squawfish. Walleye generally spawn in a discrete period during April to May, at temperatures of 4.4-14.4 °C; they are broadcast spawners and do not protect the eggs (Marshall 1977). Because metabolic requirements are relatively low at spawning temperatures, and time and energy is not spent on parental care of offspring -- spawning probably does not greatly depress overall consumption rates of walleyes in John Day Reservoir.

Consumption rates of male largemouth bass are depressed during the spawning season due to their territorial nest guarding behavior (Heidinger 1976; Adams et al. 1982). In the Hanford reach of the Columbia River, adult smallmouth bass entered sloughs as water temperatures increased in mid-March and remained there until August; spawning occurred during April-July and males guarded nests until late July (Montgomery et al. 1976). Successful hatching of smallmouth bass eggs was observed during July and August in the Hanford reach at temperatures of 15.5 to 29.5°C (Henderson and Foster 1956). We observed high consumption rates of smallmouth bass during July and August; however, since sex determinations were not made, it is possible that the nest-guarding males were differentially vulnerable to sampling and these rates (Figure 31) were more representative of the female fraction of the population. Male channel catfish are also known to build and guard nests, and to aerate and care for the eggs with body and fin movements (Scott and Crossman 1973). A discontinuation of feeding has been observed during the spawning season of channel catfish (Bailey and Harrison 1945; Clemens and Sneed 1957).

Predator Size (Age) Relations

Consumer size is an important consideration for predator-prey relations in terms of distribution, swimming ability, capture efficiency, size of prey fish consumed, metabolic requirements, conversion efficiency, growth rates, spawning and sex-ratio, and intra-specific behavioral interactions. Swimming ability of fish is known to be a function of size and species, and this fact is relevant to the distribution and movements of fish in John Day Reservoir -- especially with respect to predators inhabiting the swift currents of McNary Dam

tailrace. Poe et al. (In Press) found prey size selectivity was related to predator size in John Day Reservoir. In general, food conversion efficiency and growth rates of fish decrease with age (Brett and Groves 1979).

Northern squawfish was the only predator in John Day Reservoir which exhibited an increasing ration with fish size (age) -- over almost the entire size range, with the exception of the oldest fish (Figure 5). This aspect of the consumption relations, in conjunction with the age-structure of the population has important ramifications to the dynamics of predation in John Day Reservoir (Rieman and Beamesderfer In Press). The mean size of northern squawfish captured in McNary Dam RZ (997 g) was significantly ($P < 0.01$) greater than in the remainder of the reservoir (772 g); and the proportion of females at McNary Dam RZ is very high (Vigg and Prendergast In Preparation). The differential distribution of larger fish observed at McNary Dam is probably related to both swimming ability and size-related dominance feeding. The differential sex ratio may be an artifact of size -- since females grow faster and attain a larger size than males (Rieman and Beamesderfer In Press). Channel catfish are known to exhibit a feeding hierarchy -- in an aquaculture situation large fish were dominant in feeding, and small fish had to wait (Randolf and Clemens 1976). Large northern squawfish and channel catfish are probably dominant over their smaller counterparts at prime feeding locations at McNary Dam. The overall effect of large channel catfish on salmonid losses to predation is probably not as great, however, since their ration declines in older fish (Figure 6).

Mean prey fish ration of walleyes peaked at one year of age (Figure 7); this is probably due to their piscivorous nature which commences at an early age, combined with high growth rates. Since maintenance ration has been shown to be independent of walleye size over the range of 170-889 g (Ware 1972), the decreasing ration with age that we observed is probably related to the observed decreasing growth rates in older fish (Connolly and Rieman In Press). Smallmouth bass total prey fish and salmonid ration was highest at ages 2-4 with subsequent declines. This is consistent with the size specific consumption relations for largemouth bass i.e., their maximum daily ration declined exponentially with predator weight (Niimi and Beamish 1974).

Diel Feeding Chronology

Several factors affect the time of day that fish predators feed, including: (1) hunger and appetite, (2) metabolic requirements, (3) innate behavioral periodicity, (4) optimization of sensory organs (e.g., vision), (5) timing and intensity of light sources (e.g., sun, moon, and artificial light) (6) other physical environmental factors (e.g., temperature, flow, turbidity), and (7) factors in the biotic environment, especially prey availability. Jenkins and Green (1977)

reviewed methodology and terminology used in diel fish feeding studies. They defined commonly used terms to clarify the vocabulary and provide criteria for use: pattern describes the existence of traits characterizing a behavior; chronology describes the arrangement of feeding with time; periodicity, rhythm, and cycle are synonymous -- describing a recurrent change in activity attributable to extrinsic or intrinsic factors. Keast and Walsh (1968) documented that various species (peroids, centrarchids, and ictalurids) exhibit different diel feeding periodicities. Thus, the observed diel feeding periodicity of predators in a given environment is probably a function of both innate behavioral patterns and vulnerability patterns of prey fish.

Northern squawfish have been described as visual feeders (Eggers et al. 1978), however, little information is available on detailed feeding behavior of northern squawfish or their visual acuity as a function of light. We have observed, under laboratory conditions, that feeding activity was enhanced by low light levels (unpubl. data). In two British Columbia lakes, peak activity of northern squawfish feeding occurred in the hours of dusk and darkness (Steigenberger and Larkin 1974). The diel feeding activity we determined in John Day Reservoir indicated a pronounced difference in the feeding chronology between the McNary Dam RZ and the remainder of the reservoir. We hypothesize that this difference was due, at least in part, to differences in prey availability. On a daily basis, consumption rates of northern squawfish in McNary Dam RZ was related to smolt density (Vigg 1988).

The diel activity pattern of the prey fishes in John Day Reservoir is not well understood, however, some information on diel juvenile salmonid passage through dams is available. Most (85-95%) of yearling chinook salmon and steelhead pass McNary Dam during dusk to dawn (Long 1968). Similarly, Johnson et al. (1986) found that usually 75 to 95% of the turbine passage for salmonid smolts occurred at night at John Day Dam. Further down river at Bonneville Dam's first powerhouse, two peaks in salmon and steelhead smolt passage were observed -- a minor mode occurred after dawn (0600-1000 hours), and a much larger mode occurred at dusk, i.e., after 2000 hours (Gessel et al. 1986). Thus, the nocturnal mode in northern squawfish feeding we observed at McNary Dam RZ may be associated with increased availability of juvenile salmonids passing the dams during this period.

Another explanation for the nocturnal feeding mode of northern squawfish on smolts in McNary Dam RZ but not in the main reservoir, may be that artificial lighting at the dam extends the "twilight" period and thus enhances northern squawfish visual feeding and diminishes the nocturnal "cover" of the smolts. Low light conditions generally give visual predators an advantage over their prey (Helfman 1986; Howick and O'Brien 1983). Vogel and Smith (1985) speculated that nocturnal predation by Sacramento squawfish on chinook salmon smolts at the Red Bluff Diversion Dam, California was reduced when dam lights were turned off.

The daytime feeding of northern squawfish in the John Day Pool may

reflect the diel feeding and activity pattern of both salmonid and resident juvenile prey fishes within the reservoir. Based on the results of concurrent sampling of the turbines at John Day Dam and diel purse seining in John Day Reservoir, Sims et al. (1976) concluded that movement of juvenile salmonids through John Day Reservoir is during the daylight hours and dam passage is at night. Juvenile coho salmon in the coastal marine environment had food in their stomachs throughout the day, with a substantial increase in fullness in late afternoon and shortly after sunset (Brodeur and Pearcy 1987). Continuous feeding throughout the day has been observed for larvae, fry, and fingerling largemouth bass (which is different than the adult pattern); feeding patterns closely corresponded to their diel pattern of activity (Laurence 1971; Elliot 1976). Yellow perch and pumpkinseed, studied in littoral zone enclosures in a Canadian Lake, exhibited peaks of gut fullness between 0700-1100 hours (Hansen and Leqgett 1986). Prickly sculpins in Lake Washington exhibited peak feeding activity in the morning (0800) with subsequent declines, however they were also active at night (Rickard 1980). Thorpe (1977) found that eurasian perch consume the bulk of their food in Loch Leven, Scotland during daylight hours.

Walleye are generally considered visual feeders, but their feeding activity greatest during low light conditions. Larval and juvenile walleye were characterized as visual "strike" feeders; they exhibited highest feeding intensity at dusk (2200) and lowest at dawn (0400) (Mathias and Li 1982). Adult walleye are negatively phototactic and their daily movements are primarily related to levels of subsurface illumination (Marshall 1977; Ryder 1977). The morphology of the retina of walleye is adapted for functioning efficiently in low light in contrast to that of perches (*Perca* spp.) which is adapted to high light (Ali and Anctil 1977; Ali et al. 1977). Co-evolved diel movements and depth distributions of walleye and their prey (e.g., yellow perch) and the resultant period of spatio-temporal overlap may be considered a symbiotic predator-prey relationship based on differential visual acuity according to light intensity (Hassler and Villemonte 1953; Ali et al. 1977).

The diel feeding periodicity we observed for walleye in John Day Reservoir was bimodal, with daytime and nocturnal feeding. Thus the innate pattern, related to functional morphology, may be moderated by environmental factors. In a previous study, walleye in John Day Reservoir exhibited a consistent crepuscular pattern of stomach fullness index throughout the year -- with peaks at sunrise (0600-0800) and after sunset (2000-2200 hours) (Maule 1983; Maule and Horton 1984). Maule's chronology, however, did not account for differential seasonal digestion rates in order to back-calculate when food items were ingested. Walleye in the mid-Columbia (above McNary Dam) are believed to inhabit relatively deep water during the day, and are most vulnerable to angling when they move inshore at dusk (Williams and Brown 1975). The more variable diel chronology we observed, was similar to that reported by Swenson and Smith (1973). Walleye feeding pattern

in Lake of the Woods was uniform throughout the diel period during June, but was consistently highest at night and early morning (2000-0800 hours) during July-September; predominance of nocturnal feeding and species composition of prey showed that walleye were pelagic feeders, especially during July and August (Swenson and Smith 1973; Swenson 1977).

Largemouth bass is primarily a sight feeder (Nyberg 1971). Largemouth and smallmouth bass exhibited endogenous crepuscular activity rhythms under controlled laboratory conditions; smallmouth bass avoided bright light, and their peak activity periods occurred at the beginning and end of the dark periods (Reynolds and Casterlin 1976). In John Day Reservoir, smallmouth bass showed a crepuscular pattern; but it was not pronounced, and an extended period of morning feeding was observed. This daytime feeding may be associated with prey availability; Stauffer et al. (1976) postulated that smallmouth bass activity and distribution patterns were in response to forage fish movements. In Ontario lakes, smallmouth bass fed opportunistically during the daytime in shallow water, but peak feeding activity occurred at dusk and dawn; at night they moved into deeper water and were inactive, apparently resting (Emery 1973). Cochran and Adelman (1982) observed a nocturnal decline in consumption rates of largemouth bass in a Minnesota lake. Largemouth bass in various habitats have exhibited two diel peaks of feeding activity occurring at dawn and dusk (Snow 1971; Olmsted 1974; Perez Martinez et al. 1985). In contrast, Zweigacher and Summerfelt (1973) observed a mid-morning and afternoon period of increased feeding of largemouth bass in an Oklahoma reservoir.

Ictalurids are generally considered to be nocturnal feeders; morphological characteristics of these fishes (e.g., barbels, well developed taste buds, and small eyes) are indicative of tactile, benthic feeding. Black hullheads in a Wisconsin stream had two distinct feeding periods: the major peak occurring just before dawn, and a minor peak just after dark (Darnell and Meierotto 1962). Brown bullheads in an Ontario lake were apparently exclusively nocturnal in their feeding (Keast and Welsh 1968). Channel catfish, however, may feed both at night and during the day (Bailey and Harrison 1945), apparently using both sight and taste feeding. Our results show peak feeding of channel catfish, on both salmonid and non-salmonid prey fish, at dawn; and a minor peak at dusk. This crepuscular pattern suggests light intensity and visual feeding may be important in regulating feeding activity of channel catfish in John Day Reservoir.

Total Daily Ration

Total daily food intake by fish is basic to their growth relations, population energetics, and ultimately ecosystem production. Daily ration varies according to numerous factors, including: consumer species, size, and physiological state; quantity and quality of

available prey; digestion rates; and abiotic environmental variables (e.g., temperature and photoperiod). For example, ration estimates of marine fish predators ranges from annual means of $3 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ for an omnivore in the Bering Sea at temperatures of $2-3^{\circ}\text{C}$ (Dwyer et al. 1987), to $114 \text{ mg} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ for a planktivorous species with a high evacuation rate which would enable it to have several such feedings per day (Leong and O'Connell 1969). The range of variation in consumption rates (with respect to time, area, and predator age) that we quantified for the four fish predators in John Day Reservoir is consistent with previous determinations of comparable freshwater and anadromous species (Table 9). The mean seasonal ration of the four piscivores in John Day Reservoir ranged from 13 to $29 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$. Judging from previous estimates of temperate zone fishes, these estimates are probably conservative -- the mean daily ration estimates of temperate fishes was $59 \text{ mg} \cdot \text{g}^{-1}$ ($18-173 \text{ mg} \cdot \text{g}^{-1}$), and for tropical fishes was $167 \text{ mg} \cdot \text{g}^{-1}$ ($41 \text{ to } 360 \text{ mg} \cdot \text{g}^{-1}$) (Pandian and Vivekanandian 1985). The seasonal mean northern squawfish ration of $14.1 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ we estimated in John Day Reservoir is within the range that Falter (1969) estimated for northern squawfish in the St. Joe River, Idaho during the summer season, i.e., $10.7-15.2 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$.

The overall seasonal daily ration of walleye in John Day Reservoir ($14.2 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) was nearly equal to that of northern squawfish. The range of mean monthly daily ration of walleye in John Day Reservoir ($2 \text{ to } 40 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) is similar to that estimated for walleyes in Lake of the Woods ($8 \text{ to } 31 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) (Swenson and Smith 1973) and in Shagawa Lake and Western Lake Superior ($15 \text{ to } 40 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) (Swenson 1977); the latter studies did not have any spring samples when we observed minimum consumption rates. The temporal maximum we observed in July was concurrent with that reported by Swenson (1977). In Lake of the woods, Swenson and Smith (1973) observed maximum consumption by walleye during August and September, but attributed it to prey density.

Ware (1972) found that assimilation efficiency of walleyes feeding on fish was very high (about 96%), was not affected by temperature, and was constant over a range of meal sizes ($7 \text{ to } 52 \text{ mg} \cdot \text{g}^{-1}$); however, it decreased linearly as predator weight increased and was lower (about 83%) for invertebrate food with chitinous exoskeletons. Since walleyes of all sizes in John Day Reservoir eat over 99% fish -- we can infer that a high percentage of what is ingested is available for energetic requirements of walleye, but that proportion decreases with age.

Smallmouth bass are highly piscivorous in John Day Reservoir and have the highest total daily ration, i.e., $28.7 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$; however, their consumption rate on salmonids was very low. The higher ration of this species in John Day Reservoir may be due to the fact that the population size structure is much smaller than that of the other predators. The lack of predation on salmonids is consistent with long term studies of an Ontario lake, which have shown that smallmouth bass introductions have had no major impact on the salmonid community

Table 9. Comparison of daily rations ($\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) of various anadromous and freshwater species reported in the literature.

Family/ Species	Daily Ration	Conditions	Reference
<u>Salmonidae:</u>			
Sockeye salmon	0.1-44.1	Lake Washington, WA; Juveniles; dry weight; varied by fish weight and season.	Doble and Eggers (1978)
	28	Maximum average ration at optimum temperature of 15-17 C; dry weight; 30-40 g consumers.	Brett and Higgs (1970)
		Maximum daily ration dry weight; by size of consumer:	
	169	4g	
	43	216 g	
Coho salmon	24-37	Coastal waters, OR; wet weight; 11.4 and 13.7 C.	Brodeur and Percy (1987)
<u>Cyprinidae:</u>			
Northern squawfish		St. Joe River, ID; wet weight; varied by size for seasons:	Falter (1969)
	1.0-4.0 10.7-15.2	winter summer	
	1.2-3.9	Lake Washington, WA; wet weight; > 300 mm consumers; varied by season.	Olney (1975)
<u>Percidae:</u>			
Walleyes	5.2-5.5	Maintenance ration; dry weight; 170-889 g consumers; 12.0 C.	Kelso (1972)

Table 9. (continued)

	7.5-30.5	Lake of Woods, YN; wet weight; > 200 mm consumers; Jun to Sep.	Swenson and Smith (1973)
	15.0-39.5	Shagawa Lake, MN; wet weight; > 200 mm consumers; Jun to Sep.	Swenson (1977)
	19.5-22.8	Western Lake Superior; wet weight; > 200 mm consumers; Jul to Sep.	
	40-60	Sparkling Lake, WN; maximum daily rates; bioenergetics model.	Lyons and Magnuson (1987)
	14-82	Laboratory and field; wet weight; 36-138 mm consumers; 17.8-23.0 C.	Mathias and Li (1982)
Sauger	11.8-26.6	Lake of the Woods, MN; wet weight; > 200 mm consumers; Jun to Sep.	Swenson and Smith (1973)
	25-96	Watts Bar Reservoir, TN; wet weight; one to two year old consumers.	Minton and McLean (1982)
	0.5-37.7	Ohio River, OH; wet weight; Jan to Nov; 2.9-27.4 c.	Wahl and Nielsen (1985)
Eurasian _perch	31.9-66.9	Loch Leven, Scotland; wet weight; > 200 mm consumers; Jun to Sep.	Thorpe (1977)
<u>Centrarchidae:</u>			
Largemouth bass		Maximum Ration varied by temperature and consumer size: <u>18°C:</u>	Niimi and Beamish (1974)
	100	8g	
	30	150g	

Table 9. (continued)

		<u>30°C:</u>	
	140	8g	
	60	150g	
	13-59	Lake Rebecca, MN; wet weight; 4-27 C.	Cochran and Adelman (1982)
	4-11	Parr Pond, SC; heated effluent; poor growth; bioenergetics model.	Rice et al. (1983)
	6.2-26.0	Knox Lake, OH; varied by consumer age; bioenergetics model.	Carline (1987)
Bluegill	35.9	Maximum daily ration; wet weight; meal worms; 30 day period.	Gerking (1955)
Bluegill	13.8-22.0	Maple & Grove Lakes, MN; wet weight; summer	Seaburg and Moyle (1964)
Pumpkinseed	6.1-13.8		
Black crappie	5.8-21.2		
<u>Ictaluridae:</u>			
Channel Catfish		Aquaculture; ration for maximum growth at temperature:	Andrews and Stickney (1972)
	60	30-34°C	
	40	22-26°C	
	20	18°C	

(Martin and Fry 1972). The total daily ration of channel catfish in McNary Tailrace was composed of a larger proportion of fish (89%) than in the remainder of the John Day Pool (56%). This observation is consistent with the findings of Stevens (1959) that channel catfish were highly piscivorous in the tailrace of a South Carolina reservoir. The overall ration of channel catfish ($12.6 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) was similar to that of northern squawfish and walleye.

Limitations of Data and Consumption Estimate

This paper is based on physiological relationships of fish predators from the literature and field sampling during four years (1983-1986). During these years predator population abundances, prey fish abundances, predator diet, and environmental conditions were relatively homogeneous. In order to make inferences on areal, diel, monthly and annual consumption estimates we must make several implicit assumptions: (1) fish capture methods (primarily electroshocking) provided a representative sample of predators, i.e., not biased by vertical or horizontal strata; (2) the predators sampled were representative of the population within a given area and time; (3) three consecutive sampling days were representative of a month within a given area; (4) five months (April-August) were representative of the entire juvenile salmonid out-migration; (5) relatively small areas sampled were representative of much larger regions, and adequately describe the entire reservoir, and (6) species-specific digestion rate relationships determined under restricted laboratory conditions adequately describe a wide range of natural conditions with almost infinite permutations of components of factors (e.g., temperature, fish physiology, fish size, diet, species composition, meal size). Furthermore, if one wants to make inferences about subsequent years or other reservoirs within the Columbia System, additional, more tenuous assumptions must be made.

The main advantage of Swenson's technique is that it provides a fine-scale diel feeding chronology which is based on both a knowledge of the predators' digestion relationships and from detailed site-specific stomach contents and environmental information. The main disadvantages are: (1) that it is extremely labor-intensive to collect sufficient diel stomach contents data over a sufficient time period to incorporate a range of environmental conditions, and (2) that since it is based on pooled stomach contents and consumption per average predator, it is not possible to directly calculate variance of the estimate. Furthermore, the variance of evacuation rate relations may be substantial, but are usually not quantified rigorously enough (especially multivariate regressions) to incorporate into the consumption estimate variance. An alternate method, based on consumption per individual predator, was developed by the senior author to calculate the sample variance of the consumption estimates -- and is presented in the paper on absolute salmonid loss estimates (Rieman et al. In Press).

Management Implications

The differences in consumption rates of the four major piscivores (in terms of size relations, diel, monthly, and spatial trends) suggest ways the hydropower system, salmonid out-migrations, and fishery exploitation may be managed to ameliorate juvenile salmonid losses to predation in John Day Reservoir. Several aspects of northern squawfish consumption relations indicate that this species has a major predatory impact on juvenile salmonids, i.e.: a high overall consumption rate; exceptionally high consumption rates in McNary Dam RZ where smolts are concentrated; highest monthly consumption during July when smolt density is greatest; highest diel consumption during night and early morning hours, concurrent with peak smolt migrations; and, increasing daily ration with predator size. Furthermore, northern squawfish is the most abundant of the four predators studied (Beamesderfer and Rieman In Press). Thus we recommend that management actions are focused on northern squawfish, although predation by other species is also important and may be interactive with that by northern squawfish.

Direct removal of northern squawfish has been done in various places (reviewed by Brown and Moyle 1981), and the feasibility of various control measures in John Day Reservoir was evaluated by Poe et al. (1988). Our results show that, unlike the other predators, northern squawfish daily ration ($\text{mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) increases with predator size (age); therefore, large predators consume a disproportionately greater number of juvenile salmonids than small ones. The effects of northern squawfish population size structure on potential predation, and fishery exploitation are discussed by Rieman and Beamesderfer (In Press). Various management scenarios will be evaluated in a more quantitative way by using a simulation model which incorporates some of the basic predator-prey relations (Beamesderfer et al. In Press).

Altering the diel pattern of juvenile salmonid passage through McNary Dam could affect consumption rates in the tailrace, especially by northern squawfish and channel catfish. Minimum consumption rates for all four predators were observed in the late afternoon (1600-1800 hours); thus, in terms of predation reduction, this may be an optimum time of day for smolt passage. Facilities could be built at McNary Dam (and other dams in the system) to hold smolts for up to 24 hours, and release them at the optimum diel time period. This passage strategy may also result in high density pulses which would "swamp" predators and thus reduce the smolt mortality rates (Vigg 1988).

Water budget (timing of flows) is presently used as a management technique in the Columbia System -- primarily to reduce residence times of major groups of migrating smolts on a seasonal basis (Northwest Power Planning Council 1987). The present strategy is based on the observed inverse relationship between flow and travel time of juvenile salmonids (with the possible exception of subyearling chinook salmon) through reservoirs (Raymond 1969; Fish Passage Center 1986). Furthermore, Faler et al. (1988) documented that high water velocities ($> 1.0 \text{ m} \cdot \text{s}^{-1}$)

s⁻¹) below McNary Dam are avoided by northern squawfish. Baltz et al. (1987) found that Sacramento squawfish preferred mean surface and water column velocities of 0.22-0.28 and 0.10-0.19 m s⁻¹, respectively. Our results indicate that, under present conditions, increased flows during the peak migration of subyearling chinook salmon (July) may alleviate predation. Although quantities of excess water are generally not available in July, it may be feasible to increase spills during the optimal diel periods discussed above -- thereby rapidly moving high density pulses of juvenile salmonids through McNary Tailrace during diel periods when consumption rates were lowest.

Optimizing the seasonal timing of the juvenile salmonid out-migration through John Day Reservoir, and ultimately the entire Columbia System, could reduce predation mortality. Since consumption rate increases with temperature, and is generally highest for all predators during July -- the subyearling fall chinook salmon which exhibit peak migrations during July are subjected to the highest predation. Therefore, earlier releases of hatchery-produced subyearling fall chinook salmon and/or changing hatchery production to stocks of salmonids which out-migrate in the spring (e.g., steelhead, yearling chinook, and coho) could lessen juvenile salmonid losses to predation. Manipulation of environmental conditions (e.g., temperature, photoperiod, and feeding regime) during artificial spawning and rearing of salmonids can accelerate the smoltification process (Zaugg and McLain, 1976; Zaugg et al., 1986); thus hatchery practices may be used to alter optimum time of release. Faster, midriver migrations of subyearling fall chinook salmon may be associated with more complete smoltification (Zaugg et al., 1986). Since northern squawfish consumption is apparently depressed during their June spawning period, losses of 0-age chinook would probably be lessened if the migration could be shifted to an earlier run.

Summary and Conclusions

Trends of consumption rates of four fish predators in John Day Reservoir were modeled in order to evaluate their impact on seaward migrating juvenile salmonids. Northern squawfish are the most important predator on juvenile salmonids in John Day Reservoir in terms of their spatial, temporal, and size-related consumption rates. Prey density, thermal relations, and spawning activity are important factors affecting predator consumption rates. The thermal regime in John Day Reservoir is probably near optimum for northern squawfish consumption, and below optimum for the other predators. Optimum temperatures of the predators are approximately: northern squawfish, 20°C; walleye, 22.6°C; smallmouth bass, 28°C; and, channel catfish, 30°C. The total daily ration determined for predators in John Day Reservoir are consistent with the knowledge of physiological requirements, and similar studies of piscivores in other habitats. In consideration of the

seasonal, areal, diel, and predator size-related trends in consumption rates, in conjunction with the characteristics of the smolt out-migration -- several management actions to lessen losses of juvenile salmonids to fish predation in John Day Reservoir are feasible.

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References

- Adams, S.M., R.B. McClean, and J.A. Parrotta. 1982. Energy partitioning in largemouth bass under conditions of seasonally fluctuating prey availability. Transactions of the American Fisheries Society. 111:549-558.
- Ali, M.A., and M. Anctil. 1977. Retinal structure and function in the walleye (Stizostedion vitreum vitreum) and sauger (S. canadense). Journal of the Fisheries Research Board of Canada 34:1467-1474.
- Ali, M.A., R.A. Ryder, and M. Anctil. 1977. Photoreceptors and visual pigments as related to behavioral responses and preferred habitats of the perches (Perca spp.) and pikeperches (Stizostedion spp.) Journal of the Fisheries Research Board of Canada 34: 1467-1474.
- Andrews, J.W. and R.T. Stickney. 1972. Interactions of feeding rates and environmental temperature on growth, food conversion, and body composition of channel catfish. Transactions of the American Fisheries Society. 101:94-99.
- Bailey, R.M. and H.M. Harrison Jr. 1945. Food habits of the southern channel catfish (Ictalurus lacustris punctatus) in the Des Moines River, Iowa. Transactions of the American Fisheries Society 75: 110-138.
- Bajkov, A.D. 1935. How to estimate daily food consumption under natural conditions. Transactions of the American Fisheries Society 65: 288-289.
- Baltz, D.M., B. Vondracek, L.R. Brown, and P.B. Moyle. 1987. Influence of temperature on microhabitat choice by fishes in a California stream. Transactions of the American Fisheries Society 116: 12-20.
- Barans, C.A., and R.A. Tubb. 1973. Temperatures selected seasonally by four fishes from Lake Erie. Journal of the Fisheries Research Board of Canada 15: 607-624.

- Beamesderfer, R.C., and B.E. Rieman. In Press. Predation by northern squawfish, walleye, smallmouth bass, and channel catfish in a mainstem Columbia River reservoir: III. Estimated abundance and distribution of predators. Transactions of the American Fisheries Society 118:0000-0000.
- Beamesderfer, R.C., L.J. Bledsoe, B.E. Rieman, and S. Vigg. In Press. Simulation of predation by resident fish on juvenile salmonids in a mainstem Columbia River Reservoir. Transactions of the American Fisheries Society 118: 0000-0000.
- Bennett, D.H. P.M. Bratovich, W. Knox, D. Palmer, and H. Hansel. 1983. Status of the warmwater fishery and the potential of improving warmwater fish habitat in the lower Snake reservoirs. Final Report to U.S. Army Corp of Engineers. Contract DACW68-79-C0057. University of Idaho, Department of Fish and Wildlife Resources, Moscow, ID.
- Beyer, J.M., G. Lucchetti, and G. Gray. 1988. Digestive tract evacuation in northern squawfish (Ptychocheilus oregonensis). Canadian Journal of Fisheries and Aquatic Sciences 45:548-553.
- Beyer, J.M., and C.C. Burley. In Press. Gastric evacuation in smallmouth bass (Micropterus dolomieu). Canadian Journal of Fisheries and Aquatic Sciences 46:0000-0000.
- Black, E.C. 1953. Upper lethal temperatures of some British Columbia freshwater fishes. Journal of the Fisheries Research Board of Canada 10: 196-210.
- Brett, J.R. 1956. Some principles in the thermal requirements of fishes. Quarterly Review of Biology 31: 75-87.
- Brett, J.R. 1971. Satiation time, appetite, and maximum food intake of sockeye salmon (Oncorhynchus nerka). Journal of the Fisheries Research Board of Canada. 28:409-415.
- Brett, J.R., and D.A. Higgs. 1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon. Journal of the Fisheries Research Board of Canada 27:1767-1779.

- Brown, L.R., and P.B. Moyle. 1981. The impact of squawfish on salmonid populations: a review. North American Journal of Fisheries Management 1: 104-111.
- Carline, R.F. 1987. Simplified method based on bioenergetics modeling to estimate food consumption by largemouth bass and northern pike. Transactions of the American Fisheries Society 116:224-231.
- Carline, R.F., and J.D. Hall. 1973. Evaluation of a method for estimating food consumption rates of fish. Journal of the Fisheries Research Board of Canada 30:623-629.
- Clemens, H.P. and K.E. Sneed. 1957. The spawning behavior of channel catfish, Ictalurus punctatus. U.S. Fish and Wildlife Service Special Scientific Report Fisheries No. 219. 11 pp.
- Cochran, P.A. and I.A. Adelman. 1982. Seasonal aspects of daily ration and diet of largemouth bass, Micropterus salmoides, with an evaluation of gastric evacuation rates. Environmental Biology of Fishes 7:265-275.
- Colby, P.J., R.E. McNicol, and R.A. Ryder. 1979. Synopsis of biological data on the walleye: Stizostedion vitreum vitreum (Mitchill 1818). Food and Agricultural Organization of the United Nations, FAO Fisheries Synopsis 119: 1-139. Rome, Italy.
- Connolly, P.J. and B.E. Rieman. In Press. Population dynamics of northern squawfish and potential predation on salmonid smolts in a mainstem Columbia River Reservoir. North American Journal of Fisheries Management 9:0000-0000,
- Coutant, C.C. 1975. Responses of bass to natural and artificial temperature regimes. Pages 272-285. in R.H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute Washington, District of Columbia. USA.
- Coutant, C.C., and D.L. DeAngelis. 1983. Comparative temperature-dependent growth rates of largemouth and smallmouth bass fry. Transactions of the American Fisheries Society 112:416-423.

- Coutant, C.C., R.B. McLean, and D.L. DeAngelis. 1979. Influences of physical and chemical alterations on predator-prey interactions. Pages 57-68 in R.H. Stroud and H. Clepper, editors. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, District of Columbia. USA.
- Davis, G.E., and C.E. Warren. 1968. Estimation of food consumption rates. Pages 204-225 in W.E. Kicker, editor. IBP Handbook No. 3 - Methods of Assessment of fish production in fresh water. Blackwell Scientific, Oxford.
- Darnell, R.M., and R.R. Meierotto. 1962. Determination of feeding chronology of fishes. Transactions of the American Fisheries Society. 91:313-320.
- Doble, B.D. and D.M. Eggers. 1978. Diel feeding chronology, rate of gastric evacuation, daily ration, and prey selectivity in Lake Washington juvenile sockeye salmon, (Oncorhynchus nerka). Transactions of the American Fisheries Society 107: 36-45.
- Dwyer, D.A., K.M. Bailey, and P.A. Livingston. 1987. Feeding habits and daily ration of walleye pollock (Theragra chalcogramma) in the eastern Bering Sea, with special reference to cannibalism. Canadian Journal of Fisheries and Aquatic Sciences 44: 1972-1984.
- Ebel, W.J. 1977. Panel 2: Fish passage problems and solutions-major passage problems. Pages 33-39 in E. Schwiebert, editor. Columbia River Salmon and Steelhead. American Fisheries Society. Special Publication No. 10. Washington D.C.
- Eder, S., and McDannold, W.E., Sr. 1987. The channel catfish fishery at Pony Express Lake, Missouri, 1963-1984. North American Journal of Fisheries Management, 7:502-512.
- Elliot, G.V. 1976. Diel activity and feeding of schooled largemouth bass fry. Transactions of the American Fisheries Society 105: 624-627.
- Elliot, J.M. and L.L. Persson. 1978. The estimation of daily rates of food consumption for fish. Journal of Animal Ecology 47: 977-991.

- Faler, M.P., L.M. Miller, K.I. Welke. 1988. Effects of variation in flow on distributions of northern squawfish in the Columbia River below McNary Dam. North American Journal of Fisheries Management 8:30-35.
- Falter, C.M. 1969, Digestive rates and daily rations of northern squawfish in the St. Joe River, Idaho. Doctoral dissertation, University of Idaho, Moscow, Idaho.
- Fange, R., and D.J. Grove. 1979. Digestion. Pages 161-260 in Fish Physiology. W.S. Hoar, D.J. Randall, and J.R. Brett, editors. Academic Press, London.
- Ferguson, R.G. 1958. The preferred temperature of fish in their midsummer distribution in temperate lakes and streams. Journal of Fisheries Research Board of Canada 15:607-624.
- FPC (Fish Passage Center). 1988. Smolt monitoring program, annual report, 1987. BPA project No. 87-127. Fish Passage Center, Portland, OR.
- FPC (Fish Passage Center). 1988. Smolt monitoring program, annual report, 1987. BPA project No. 86-60. Fish Passage Center, Portland, OR.
- Fry, F.E.J. 1947. Effects of the environment on animal activity. University of Toronto Studies in Biology, Serial Publications Ontario Fisheries Research Laboratory 68:1-62.
- Gerking, S.D. 1955. Influence of the rate of feeding on body composition and protein metabolism of bluegill sunfish. Physiological Zoology 25:358-372.
- Gessel, M.H. L.G. Gilbreath, W.D. Muir, and R.F. Krcma. 1986. Evacuation of the juvenile collection and bypass systems at Bonneville Dam -- 1985. Annual Report to U.S. Army Corps of Engineers. Contract No. DACW57-85-H-0001. National Marine Fisheries Service, Seattle, WA.

- Hansel, H.C., S.D. Duke, P.T. Lofy, and G.A. Gray. 1988. use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. Transactions of the American Fisheries Society 117:55-62.
- Hansen, M.J. and W.C. Leggett. 1986. Effect of competition between two freshwater fishes on prey consumption and abundance. Canadian Journal of Fisheries and Aquatic Sciences 43:1363-1372.
- Hassler, A.D. and J.R. Villemonte. 1953. Observations on the daily movements of fishes. Science 188:321-322.
- Heidinger, R.C. 1976. Synopsis of biological data on the largemouth bass Micropterus salmoides (Lacepede) 1802. Food and Agricultural Organization Fisheries Synopsis 115: 1-85. Rome, Italy.
- Helfman, G.S. 1986. Behavioral responses of prey fishes during predator-prey interactions. Pages 135-156 in Predator-prey relationships. M.E. Feder and G.V. Lander, editor= University of Chicago Press, Chicago.
- Henderson, C., and R.F. Foster. 1956. Studies of smallmouth bass (Micropterus dolomieu) in the Columbia River near Richland, Washington. Transactions of the American Fisheries Society 36:112-127.
- Hjort, R.C., B.C. Mundy, and P.L. Hulett. 1981. Habitat requirements for resident fishes in the reservoirs of the lower Columbia River. Final Report. U.S. Army Corps of Engineers. Contract No. DACW57-79-C-0067, 180 p. Portland, OR.
- Howick, G.L., and W.J. O'Brien. 1983. Piscivorous feeding behavior of largemouth bass: an experimental analysis. Transactions of the American Fisheries Society 112: 508-516.
- Hokanson, K.E.F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. Journal of the Fisheries Research Board of Canada 34:1524-1550.

- Jenkins, B.W. and J.M. Green. 1977. A critique of field methodology for determining fish feeding periodicity. *Environmental Biology of Fishes* 1:209-214.
- Jobling, M. 1981. Mathematical models of gastric emptying and estimation of daily rates of food consumption for fish. *Journal of Fish Biology* 19:245-257.
- Jobling, M. 1986. Mythical models of gastric emptying and implications for food consumption studies. *Environmental Biology of Fishes* 16: 35-50.
- Johnson, R.C. L.A. Wood, and W.W. Smith. Monitoring of downstream salmon and steelhead at federal hydroelectric facilities -- 1986. Annual Report to Bonneville Power Administration. Agreement No. DE-AI-79-85BP20733. National Marine Fisheries Service, Seattle, WA.
- Keast, A., and L. Welsh. 1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of the day in some lake fishes. *Journal of the Fisheries Research Board of Canada* 25:1133-1144.
- Kelso, J.R.M. 1972. Conversion, maintenance, and assimilation for walleye, Stizostedion vitreum vitreum, as affected by size, diet, and temperature. *Journal of Fisheries Research Board of Canada* 29:1181-1192.
- Kilambi, R.V., J. Noble, and C.E. Hoffman. 1971. Influence of temperature and photoperiod on growth, food consumption and food conversion efficiency of channel catfish. *Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners* 24: 519-531.
- Koenst, W.M., and L.L. Smith Jr. 1976. Thermal requirements of the early life history stages of walleye, Stizostedion vitreum vitreum, and sauger, Stizostedion canadense. *Journal of Fisheries Research Board of Canada* 33: 1130-1138.
- Laurence, G.C. 1971. Digestion rate of larval largemouth bass. *New York Fish & Game Journal*. 18: 52-56.

- Leong, R.J.H., and C.P. O'Connell. 1969. A laboratory study of particulate and filter feeding of the northern anchovy (Engraulis mordax). Journal of Fisheries Research Board of Canada 35: 1469-1478.
- Long, C.W. 1968. Diel movement and vertical distribution of juvenile anadromous fish in turbine intakes. U.S. Fish and Wildlife Service Fishery Bulletin 66: 599-609.
- Lyons, J., and J.J. Magnuson. 1987. Effects of walleye predation on the population dynamics of small littoral-zone fishes in a northern Wisconsin lake. Transactions of the American Fisheries Society 116:29-39.
- Mann, K.H. 1978. Estimating food consumption of fish in nature Pages 250-273 in S.D. Gerking, editor. Ecology of Freshwater Fish Production. Wiley, New York.
- Marshall, T.R. 1977. Morphological, physiological, and ethological differences between walleye (Stizostedion vitreum vitreum) and pikeperch (S. lucioperca). Journal of the Fisheries Research Board of Canada. 34:1515-1523.
- Martin, N.V. and F.E.J. Fry. 1972. Lake Opeongo: effects of exploitation and introductions on the salmonid community. Journal of the Fisheries Research Board of Canada 29:795-805.
- Maule, A.G. 1973. Aspects of the life history and feeding ecology of walleye (Stizostedion vitreum vitreum) in the Mid-Columbia River. M.S. thesis. Oregon State University, Corvallis, OR.
- Maule, A.G. and H.F. Horton. 1984. Feeding ecology of walleye, Stizostedion vitreum vitreum, in the mid-Columbia River, with emphasis on the interactions between walleye and juvenile anadromous fishes, U.S. Department of Commerce. National Marine Fisheries Service. Fishery Bulletin 82: 411-418.
- Montgomery, J.C., D.H. Fickeisen, and C.D. Becker. 1980. Factors affecting smallmouth bass production in the Hanford area, Columbia River. Northwest Science 54:296-305.

- Mount, D.I. 1969. Developing thermal requirements for freshwater fishes. Pages 140-147 in: P.A. Krenkel and F.L. Parker, editors, Biological aspects of thermal pollution. Vanderbilt University Press, Nashville, TN.
- Niimi, A.J. and F.W.H. Beamish. 1974. Bioenergetics and growth of largemouth bass (Micropterus salmoides) in relation to body weight and temperature. Canadian Journal of Zoology 52:447-456.
- NPPC (Northwest Power Planning Council). 1987. Columbia River Basin Fish and Wildlife Program. Adopted November 15, 1982, ammended October 10, 1984, and February 11, 1987. Northwest Power Planning Council, Portland, OR.
- Nyberg, D.W. 1971. Prey capture in the largemouth bass. American Midland Naturalist 86:128-144.
- Olmsted, L.L. 1974. The ecology of largemouth bass (Micropterus salmoides) and spotted bass (Micropterus punctatus) in Fort Smith, Arkansas. Doctoral Dissertation. University of Arkansas. 133 p.
- Pandian, J.J., and W. Vivekanandan. 1985. Energetics of feeding and digestion. Pages 99-124 in P. Tytler and P. Catlow, editors. Fish energetics: new perspectives. John Hopkins University Press, Baltimore.
- Patten, B.G. and D.T. Rodman. 1969. Reproductive behavior of the northern squawfish, Ptychocheilus oregonensis, Transactions of the American Fisheries Society 98: 108-111.
- Perez A.M., F.P. Guerra and M. Penaz. 1985. Feeding habits of Micropterus salmoides in Cuba. Prirodoved Pr. Ustavu. Cesk. Acad. Ved. Brne. 19: 1-36. (Biosis)
- Persson, L. 1982. Rate of food evacuation in roach (Rutilus rutilus) in relation to temperature, and the application of evacuation rate estimates for studies on the rate of food consumption. Freshwater Biology 12:203-210.
- Persson, L. 1986. Patterns of food evacuation in fishes: a critical review. Environmental Biology of Fishes 16:51-58.

- Poe, T.P., H.C. Hansel, S. Vigg, L.A. Prendergast, and D.E. Palmer. In Press. Predation by northern squawfish, walleye, smallmouth bass, and channel catfish in a mainstem Columbia River reservoir: I. Feeding ecology during the salmonid smolt out-migration. Transactions of the American Fisheries Society 118:0000-0000.
- Poe, T.P., P.T. Lofy, S. Duke, A.A. Nigro, and B.E. Rieman. 1983. Feasibility of various control measures. In: T.P. Poe and B.E. Rieman, editors. Resident fish predation on juvenile salmonids in John Day Reservoir, 1983-1986. Final Report to Bonneville Power Administration, Portland, OR.
- Randolph, K.N., and H.P. Clemens. 1976. Some factors influencing the feeding behavior of channel catfish in culture ponds. Transactions of the American Fisheries Society 105:718-724.
- Raymond, H.D. 1969. Effect of John Day Reservoir on the migration rate of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. Transactions of the American Fisheries Society 108:505-529.
- Reutter, J.J. and C.E. Herdendorf. 1974. Laboratory estimates of the seasonal final temperature preference of some Lake Erie fish. Proceedings 17th Conference of Great Lakes Research 1974: 59-67. International Association of Great Lakes Research.
- Reynolds, W.W. and M.E. Casterlin. 1976. Activity rhythms and light intensity preferences of Micropterus salmoides and M. dolomieu. Transactions of the American Fisheries Society 105:400-403.
- Rice, J.A., J.E. Breck, S.M. Bartell, and J.F. Kitchell. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environmental Biology of Fishes. 9:263-275.
- Rickard, N.A. 1980. Life history and population characteristics of the prickly sculpin in Lake Washington. M.S. thesis. University of Washington, Seattle, WA. 148 p.
- Rieman, B.E. and R.C. Beamesderfer. In Press. Population dynamics of northern squawfish and potential predation on salmonid smolts in a mainstem Columbia River Reservoir. North American Journal of Fisheries Management 9:0000-0000.

- Rieman, B.E., R.C. Beamesderfer, L.J. Bledsoe, and S. Vigg and T.P. Poe. In Press. Predation by northern squawfish, walleye, smallmouth bass, and channel catfish in a mainstem Columbia River reservoir: IV. Total loss and mortality of juvenile salmonids. Transactions of the American Fisheries Society 118:0000-0000.
- Ryder, R.A. 1977. Effects of ambient light variations on behavior of yearling, subadult, and adult walleye (Stizostedion vitreum vitreum). Journal of the Fisheries Research Board of Canada 34:1481-1491.
- Sainsbury, K.J. 1986. Estimation of food consumption from field observations of fish feeding cycles. Journal of Fish Biology 29: 23-36.
- Seaburg, K.G., and J.B. Moyle. 1964. Feeding habits, digestive rates, and growth of some Minnesota warmwater fishes. Transactions of the American Fisheries Society 93:269-285.
- Shrable, J.B., O.W. Tiemeier, C.W. Deyoe. 1969. Effects of temperature on rate of digestion by channel catfish. Progressive Fish-Culturist 31 : 131-1 38.
- Shuter, B.J., D.A. Wismer, H.A. Regier, and J.E. Matuszek. 1985. An application of ecological modelling: impact of thermal effluent on a smallmouth bass population. Transactions of the American Fisheries Society 114: 631-651.
- Sims, C.W., R.C. Johnson, W.W. Bently. 1976. Effects of power peaking operations on juvenile salmon and steelhead trout migrations 1975. Processed Report, NOAA, NMFS, Northwest Fisheries Center, Seattle, WA.
- Smagula, C.M., and I.R. Adelman. 1982. Day-to-day variation in food consumption by largemouth bass. Transactions of the American Fisheries Society. 111:543-548.
- Stauffer, J.R. Jr., K.L. Dickson, J. Cairns Jr., and D.S. Cherry. 1976. The potential and realized influences of temperature on the distribution of fishes in the New River, Glen Lyn, Virginia. Journal of Wildlife Management. Wildlife Monograph No. 50.

- Steigenberger, L.W., and P.A. Larken. 1974. Feeding activity and rates of digestion of northern squawfish (Ptychocheilus oregonensis). Journal of the Fisheries Research Board of Canada 31: 411-420.
- Stevens, R.E. 1959. The white and channel catfishes of the Santee-Cooper Reservoir and tailrace sanctuary. Proceedings of the Annual Conference of Southeastern Association of Game and Fish Commissioners 13: 203-219.
- Swenson, W.A. 1972. Food competition between walleye, Stizostedion vitreum vitreum (Mitchill) and sauger, Stizostedion canadense (Smith), in Lake of the Woods, Minnesota. Doctoral dissertation. University of Minnesota, St. Paul, Minnesota.
- Swenson, W.A. 1977. Food consumption of walleye (Stizostedion vitreum vitreum) and sauger (S. canadense) in relation to food availability and physical environmental conditions in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. Journal of the Fisheries Research Board of Canada 34: 1643-1654.
- Swenson, W.A. and L.L. Smith Jr. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (Stizostedion vitreum vitreum). Journal of the Fisheries Research Board of Canada 30:1327-1336.
- Swenson, W.A. and L.L. Smith Jr. 1976. Influence of food competition, predation, and cannibalism on walleye (Stizostedion vitreum vitreum) and sauger (S. canadense) populations in Lake of the Woods, Minnesota. Journal of the Fisheries Research Board of Canada 33:1946-1954.
- Thompson, R.B. 1959. Food of the squawfish Ptychocheilus oregonensis (Richardson) of the lower Columbia River. United States Fish and Wildlife Service, Fisheries Bulletin No. 158: 43-58.
- Thorpe, J.E. 1977. Daily ration of adult perch, Perca Fluviatilis L. during summer in Loch Leven, Scotland. Journal of Fish Biology 11:55-68.
- Vigg, S. 1988. Functional response of northern squawfish predation to salmonid prey density in McNary Tailrace, Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 45:0000-0000.

- Vigg, S., and C.C. Burley. In Preparation. Temperature dependant maximum daily consumption of juvenile salmonids by northern squawfish (Ptychocheilus oregonensis). For submittal to Canadian Journal of Fisheries and Aquatic Sciences.
- Vigg, S., and L.A. Prendergast. In Preparation. Seasonal changes in gonadal-somatic index related to spawning of northern squawfish in John Day Reservoir, Columbia River. For submittal to North American Journal of Fisheries Management.
- Vogel, D.A., and J.G. Smith. 1985. Fish passage action program for Red Bluff Diversion Dam. Annual Progress Report. U.S. Fish and Wildlife Service Report No. FRI/FAO-86-5. 51 pp.
- Wahl, D.H. and L.A. Nielsen. 1985. Feeding ecology of the sauger (Stizostedion canadense) in a large river. Canadian Journal of Fisheries and Aquatic Sciences 42: 120-128.
- West, B.W. 1966. Growth, food conversion, food consumption, and survival at various temperatures of the channel catfish, Ictalurus punctatus (Rafinesque). M.S. thesis. University of Arkansas, Fayetteville, AR.
- Williams, K., and L. Brown. 1985. Mid-Columbia walleye: fisheries, life history, management 1979-1982. Washington Department of Game. Olympia, WA.
- Windell, J.T. 1967. Rates of digestion in fishes. Pages 151-173 in S.B. Gerking, editor. The Biological Basis of Fish Product?%. Wiley, New York.
- Zaugg, W.S., and L.R. McLain. 1976. Influence of water temperature on gill sodium, potassium-stimulated ATPase activity in juvenile coho salmon (Oncorhynchus kisutch) Comparative Biochemistry and Physiology 54A: 419-421.
- Zaugg, W.S., J.E. Bodel, J.E. Manning, and E. Wold. 1986. Smolt transformation and seaward migration in 0-age progeny of adult spring chinook (Oncorhynchus tshawytscha) matured early with photoperiod control. Canadian Journal of Fisheries and Aquatic Sciences 43: 885-888.

Zweiacher, P.L., and R.C. Summerfelt. 1973. Seasonal variation in food and diel periodicity in feeding of northern largemouth bass, Micropterus salmoides (Lacepede) in an Oklahoma reservoir. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 27: 579-591.

Digestive Tract Evacuation in Northern Squawfish
(Ptychocheilus oregonensis)

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Abstract

Digestive tract evacuation in northern squawfish (Ptychocheilus oregonensis) (170-1900 g) was studied in fish allowed to feed voluntarily on salmon (4-70 g) at three water temperatures (10, 15 and 20 C). Squawfish were sacrificed at 1- or 2-h intervals until evacuation approximated 90%. Amount of food evacuated for a given time interval increased approximately three times as the temperature was increased and as the prey weight was increased, and two times as the predator weight was increased. The 90% digestive tract emptying time decreased by about two-thirds as the temperature doubled and by about one-half as the predator weight increased 10 times, but approximately doubled when the prey weight increased 4 times. Two-fish meals (17-20 g each, 35-39 g total) were evacuated more slowly than meals of one fish weighing 17-20 g, but at the same rate as meals of one fish weighing 35-40 g. Equations derived are easily applied to a wide range of water temperatures, prey weights, and predator weights.

Introduction

Northern squawfish (Ptychocheilus oregonensis) are known predators of juvenile salmonids (Ricker 1941; Thompson 1953; Uremovich et al. 1980), but the extent of that predation is still in question. Reliable estimates of consumption rates from stomach or gut contents of predators are dependent upon accurate knowledge of evacuation rates (Swenson and Smith 1973; Jobling 1981). Previous studies on evacuation rates of northern squawfish, however, have not been in agreement and can result in different estimates of consumption. Uremovich et al. (1980), for instance, used Falter's (1969) evacuation equations and determined that a large squawfish (>20 cm) could eat three salmon per day at water temperature of 9.6°C. If he had used Steigenberger and Larkin's (1974) equations, he would have concluded that it could eat less than one-half salmon per day.

Attempts to apply the equations in the previous studies to field data may also lead to inaccuracies. They are based on narrower ranges of prey and predator weights than present in the field (Uremovich et al. 1980), and their results are presented in separate equations for different water temperatures and predator and prey groups, making application to intermediate values subject to error.

The objectives of our study were to develop an easily applied single, digestive tract evacuation equation applicable to a wide range of prey sizes, predator sizes, and water temperatures and to attempt to resolve inconsistencies between the conclusions made in previous studies on evacuation in northern squawfish.

Methods and Materials

Laboratory Experimentation

In order to minimize correlations between the variables examined, predator and prey were divided into three size groups and each combination of predator and prey size was tested at each water temperature. Up to three replicates were obtained at 1- or 2-h intervals for each combination of prey group, predator group, and water temperature until evacuation approximated 90%.

Experiments were conducted from July 1983 to August 1985; northern squawfish used in the experiments were collected periodically as needed by electrofishing the John Day Dam tailrace in the Columbia River. Two or three predators were selected at random from each size group (250-349, 350-399, and 400-560 mm FL) and placed in each of seven circular tanks (capacity 2,200 L). Size groups within each tank were separated by screen dividers. The squawfish were acclimated by changing their water temperature at the rate of 1/2 C per day until the selected temperature was reached and then holding them at the desired temperature for a minimum of one week prior to experimentation. During this time, the squawfish were fed live juvenile salmon ad libitum. Prior to experimentation, the squawfish were starved 72-96 h, the time necessary to empty their digestive tracts based on preliminary trials.

Prey fish were obtained from the Willard National Fish Hatchery, Cook, Washington. Chinook and coho salmon (Oncorhynchus tshawytscha and O. kisutch) were used interchangeably based on availability. Prior to experimentation, small sections of stainless steel wire (5 mm long; to experimentation, small sections of stainless steel wire (5 mm long; 0.5 mm diameter) were injected in the head and caudal peduncle of salmon and magnetized with a Quality Control Device (QCD) so that squawfish that had eaten the salmon could be identified with a metal detector. One preweighed (+0.1 g) salmon from the selected size group (4-15, 15-35, and 35-70 g) was placed in each tank section 0.5-h before daylight. The sections were checked at 0.5-h intervals and ingestion time was considered to be the midpoint of the interval during which feeding occurred. After a predetermined time, the predator in each section was identified, weighed (+1.0 g), and measured. The entire digestive tract was removed and the contents of the tract were blotted, weighted (+0.1 g), and preserved in 10% formalin. To obtain a relationship between preserved and fresh weights, which could be applied to preserved field contents, we reweighed a subsample of the digestive tract contents after a minimum of 2 wk in formalin.

The effect of the body of the prey not being entirely in the digestive tract during the initial stages of digestion (as evidenced by the tail of the prey protruding from the mouth of the

predator) was also examined. To enable us to estimate the maximum length of prey that would fit in the anterior limb of the digestive tract, that part of the tract was stretched and measured on a subsample of northern squawfish.

The effect of feeding two-fish meals was assessed at a single water temperature (15 C), time since feeding (4 h), and predator size (400-560 mm). Predators were fed one-fish meals (17-20 g) or (35-40 g), or two-fish meals (17-20 g each, 35-39 g total). Six replicates were obtained in each category.

Data Analysis

The frequently used decay model (percent of food remaining in the tract as the dependent variable) was compared to a growth model (weight evacuated as the dependent variable) using the coefficients of multiple determination (R^2) adjusted for degrees of freedom and residual plots as criteria.

The all-possible-regression selection procedure with C_p criterion (Neter et al. 1983) was used to select the best subset of independent variables, with the goal of achieving a C_p value close to the number of independent variables selected. A correlation matrix was obtained to determine interactions between variables.

Possible transformations were evaluated for fit and ability to meet the linear least squares analysis assumptions of homogeneity of variance, normality, and independence of errors. The mean square residual (MSR) with untransformed values and residual plots were used as criteria for the comparison.

The relation between the length of the anterior limb of the intestine and the length of northern squawfish was determined by linear regression. The largest prey that would fit in the anterior limb of the intestine was computed by using the length of the limb as the standard length (SL) of a salmon and estimating the weight of the prey from equations given by Gray et al. (1983). Standard length (SL) was used because little of the tail of the prey would be expected to digest.

We used tests to compare the evacuation (g) of two-fish meals with the evacuation of one-fish meals. To validate the prediction equations, we compared the mean grams evacuated in the one-fish meals with predicted means and the 95% confidence intervals for an additional six samples.

The relation between fresh and preserved weights was determined by linear regression and by averaging the percent change in weight.

Results

Evacuation Equation

All the independent variables tested were selected as predictors of evacuation. The four variables, time, water temperature, prey weight and predator weight (listed in order of decreasing importance) resulted in a C(p) of 5.0. The variables were not highly correlated, with all correlations less than 0.50.

Digestive tract evacuation expressed in weight evacuated provided better fits (R^2 0.77-0.90) than did the models in which evacuation was expressed as percent of food remaining (R^2 0.36-0.52). The best fitting equation resulted from log transformations of all the variables, (Table 1) (Fig. 1). That equation, in exponential form was:

$$(1) \text{ Weight evacuated} = 0.0013 \, t^{0.93} \, s^{0.43} \, T^{1.49} \, W^{0.25}, \\ R^2 = 0.902, \, n = 284$$

where t is time (h), S is prey weight (g), T is temperature ($^{\circ}\text{C}$), and W is predator weight (g). Examination of the residual plots showed that the log transformation of grams evacuated improved homogeneity of variance.

The evacuation rate (ER), in grams per hour, was nearly constant over time (the exponent of time was close to 1.00) and increased with increasing water temperature, prey weight, and predator weight. An equation to predict the average rate was derived by regressing the log of the ratio of grams evacuated per hours evacuated with $\ln(S)$, $\ln(T)$, and $\ln(W)$:

$$(2) \text{ ER} = 0.0010 \, S^{0.39} \, T^{1.57} \, W^{0.26}, \\ R^2 = 0.75, \, n = 284$$

When this equation was used over the range of the data, predicted values of the average ER increased by 3.0 times as the temperature was raised from 10°C to 20°C , by 3.1 times as the prey weight was increased from 4 to 70 g, and by 1.8 times as predator weight was increased from 173 to 1943 g (Fig. 2).

The time required for 90% emptying time (ET_{90}) decreased with increasing temperature and predator weight but increased with increasing prey weight. At 90% evacuation, \ln (grams evacuated)

Table 1 . Comparison of the equations describing digestive tract evacuation in northern squawfish (, indicated a logarithmic transformation).

Model	Fit		Coefficients				
	R^2	MSR	Intercept	Time (h)	Prey (g)	Temp (°C)	Pred (g)
Evacuation (g)							
linear	0.78	18	-16.8	0.76	0.24	0.81	0.0045
square root	0.84	16	-1.4	0.13	0.04	0.13	0.0006
exponential	0.77	40	-1.5	0.10	0.02	0.11	0.0004
log-log	0.902	8	-6.7	0.93	0.43	1.49	*0.2500
	0.900	8	-2.8	*0.91	0.44	0.10	0.0004
	0.89	9	-2.7	*0.92	0.48	0.10	

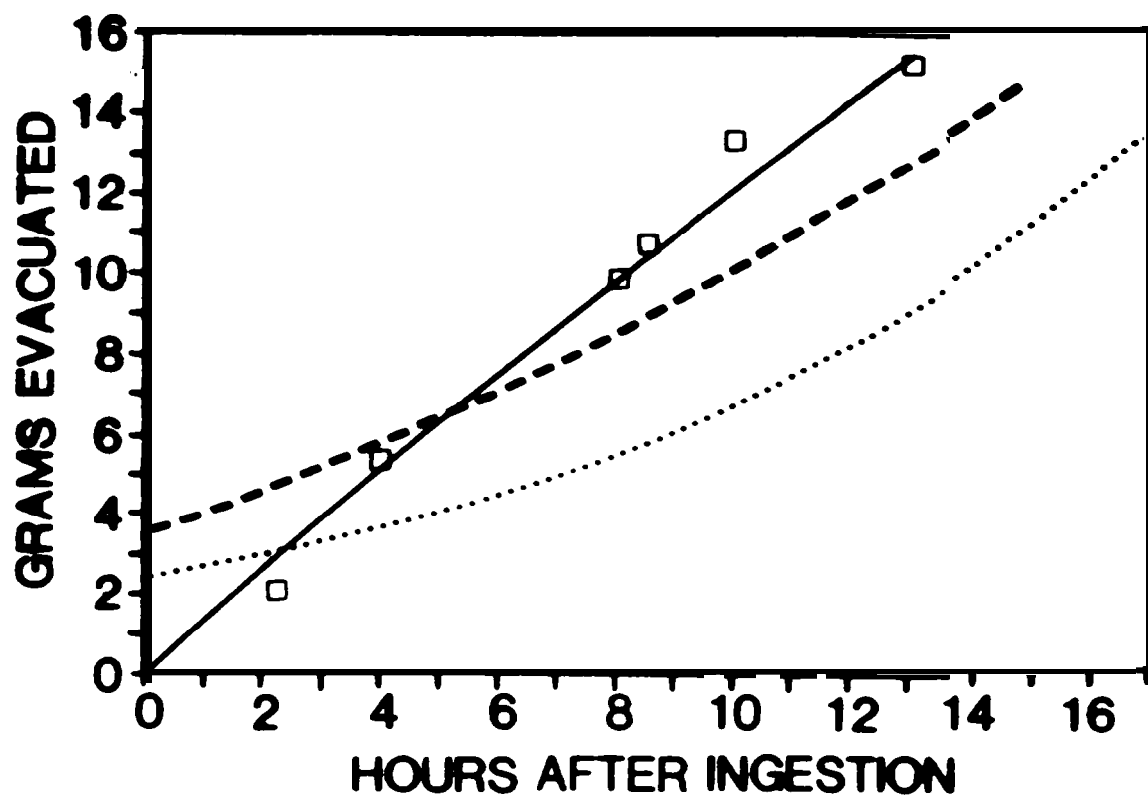


Fig. 1. Comparison of the fit of the square root (---), logarithmic (···), and log-log (---) equations for 15- to 20-g prey, 15°C, 800-g predators. \square = one to three samples.

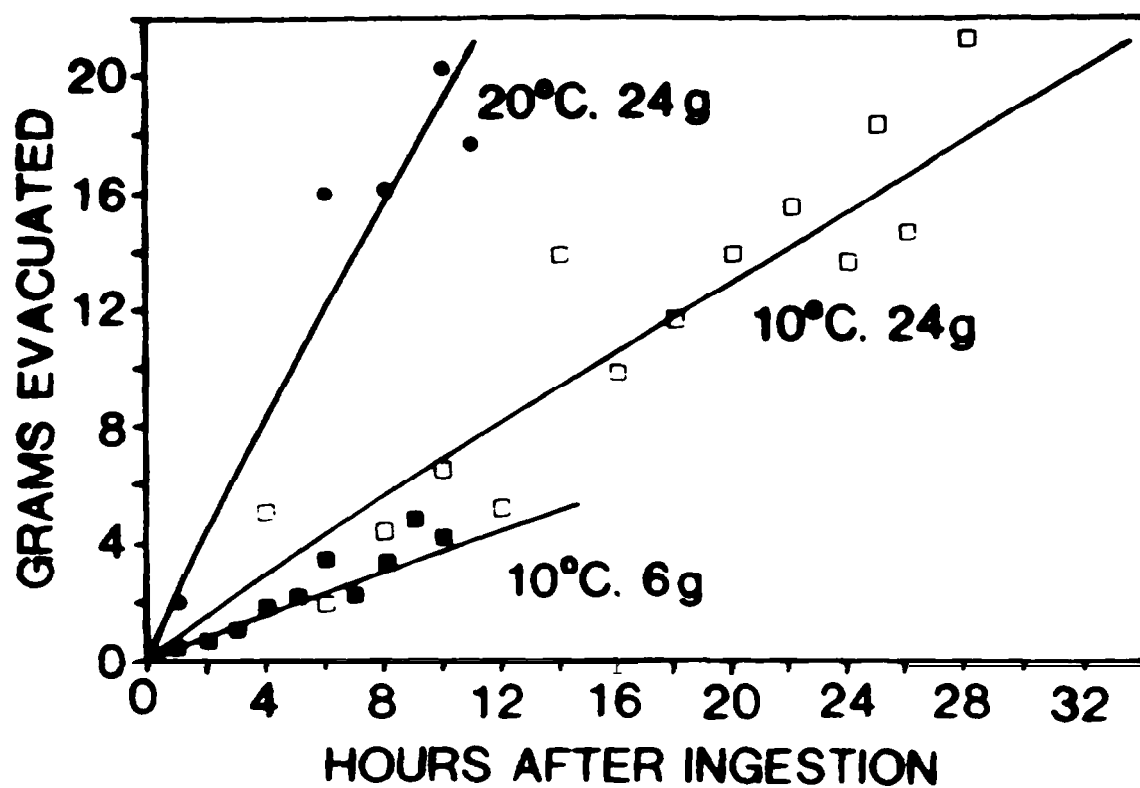


Fig. 2. Comparison of the effects of increasing water temperature from 10 to 20°C and prey weight from 6 to 24 g on the evacuation rates and emptying times (90%) in northern squawfish (symbols = one to three samples).

would be ln (0.9 s) and substituting this in equation (1) would give:

$$(3) \quad ET_{90} = 1147 S^{0.61} T^{-1.60} W^{-0.27}.$$

The ET_{90} predicted from equation (3) slightly more than doubled as the prey weight increased 4 times, but decreased by about two-thirds when the temperature doubled (Figure 2). Predator weight had less effect; a 10 x increase in the predator weight approximately halved the ET_{90} . Predicted 90% evacuation times ranged from 3 h (4-g prey, 20°C, 1500-g predator), to 67 h (70-g prey, 10°C, 640-g predator).

The entire range of prey sizes could not be tested for all predator sizes (Table 2) because the small predators either 'were unable to eat the large prey or regurgitated soon after swallowing. This resulted in a correlation ($r = 0.38$) between prey and predator size. The relationship was found between fish length and the length of the anterior limb of the intestine was linear over the sizes of predators investigated:

$$\text{Anterior limb (mm)} = -45 + 0.48 \text{ predator (mm FL)} \\ r^2 = 0.94, n = 8$$

As judged by this regression, the largest prey body that would fit in the anterior limb of the digestive tract of a predator 434 mm long, weighing 948 g, and having a condition factor of 1.16 would be 173 mm and 59 g (6% body weight). Predators ate up to 11% body weight (Table 2). Analyses in which meal sizes were less than 6% of the body weight showed only minor changes in the regression equations---indicating that little bias resulted from the body of the prey not being entirely in the digestive tract.

Two-Fish Meals

Weight evacuated 4 h after the feeding of two-fish meals (17-20 g each, 35-39 g total) was significantly greater ($P < 0.05$) than weight evacuated after the feeding of one-fish meals weighing 17-20 g, but was not significantly different from evacuation after the feeding of one-fish meals weighing 35-40 g. Evacuation of one-fish meals (17-20 g) averaged 5.4 g (SE 0.98), and evacuation of one-fish meals (35-40 g) and two-fish meals (35-39 g total) averaged 7.9 g (SE 4.3) and 7.8 g (SE 1.6), respectively. Predator weights were not significantly different between groups compared.

Table 2. Means and (in parentheses) ranges from northern squawfish one-fish meal experiments by prey size group: small (4-14 g), medium (15-34 g), and large (35-70 g).

Prey Size (Sample Size)	Predator			Prey (g)	Meal (% Body wt)
	Weight (g)	(FL mm)	Condition Factor		
Small	596	375	1.08	6	1
(130)	(173-1497)	(255-559)	(0.61-1.52)	(4-14)	(0-5)
Medium	695	389	1.12	24	4
(107)	(305-1733)	(305-511)	(0.64-1.50)	(15-34)	(1-9)
Large	954	434	1.13	45	5
(47)	(420-1943)	(348-538)	(0.74-1.61)	(35-70)	(2-11)

Validation of the Prediction Model

The mean weight evacuated obtained in the one-fish meals were very close to those predicted by the evacuation equation and within the 95% confidence intervals (CI) for the mean of an additional six samples. When mean prey and predator weights were used, Equation (1) predicted evacuation of 5.3 g (3.9 - 7.2 g CI) compared with the 5.4 g obtained in the one-fish meals for the 18.5-g prey (1047-g predator), and predicted 7.2 g (5.0 - 10.4 g CI) compared with the 7.9 g obtained for the 37.7-g prey (1029-g predator).

Effects of Preservation

Preservation in 10% formalin resulted in an average 4% weight reduction. The equation:

$$\text{Fresh (g)} = 0.008 + 1.04 \text{ Preserved (g)}$$
$$r^2 = 0.998, n = 106$$

should be applied to preserved digestive tract contents before the prediction evacuation equations are used.

Discussion

Ecological Implications

Our single equation model makes possible more accurate estimates of salmonid consumption by northern squawfish. It also allows more precise determination of how consumption varies with different water temperatures, sizes of salmon, and sizes of squawfish. Our results, for instance, indicate that the size of the meal eaten greatly affects the number of meals that can be eaten per day. Previous studies on northern squawfish evacuation either assumed that the size of the meal had no effect (Falter 1963) or did not test the effects of meals greater than 11 g (Steigenberger and Larkin 1974).

We also determined that evacuation rates, and potentially consumption rates, are faster at 10°C than indicated by the equations of Steigenberger and Larkin (1974). Using our equation, for example, Uremovich et al. (1980) would have found that a 300-349 mm FL northern squawfish could eat seven to eight 8 g meals per day at 10°C; using Steigenberger and Larkin's (1974) equation, they would have predicted it could eat less than one 8 g meal per day. Other studies on squawfish evacuation at 10°C agree with our determination. Vondracek (in press) studied the effects of temperature on the total evacuation times of salmon in a similar species, the Sacramento squawfish (Ptychocheilus grandies), and estimated that the emptying time at 10°C was 38 h, less than the 51-141 h predicted by Steigenberger and Larkin's (1974) equations. Our estimate of 100% evacuation time at 10°C, using a similar meal (14.8 g) and predator size (822 g) was 29 h, however, even less than Vondracek's estimate. This could be attributed to the difference in species or the fact that he force fed salmon to the squawfish. Falter's (1969) work and Steigenberger and Larkin's (1974) field study results appear very similar to ours. Falter's (1969) equation, based on unstated sizes of prey fish, also predicts a 24 h emptying time at 10°C. Steigenberger and Larkin (1974) found that two-thirds of the squawfish that they held in the field, averaging about 10 g in their tracts to start, had empty digestive tracts after 24 h at 10-12°C. It is difficult to determine the reason for Steigenberger and Larkin's (1974) unusual laboratory results. They only allowed overnight acclimation to each temperature, but the fish were held at 10-13°C prior to acclimation. It is apparent, however, that consumption estimates based on their equations at the colder temperatures are underestimates of the actual consumption taking place.

Biological Implications

Comparison with other piscivorous fish

Although relations between mathematical descriptions of evacuation in fish and the underlying biological/physiological processes are not well understood (Jobling 1986), it might be expected that evacuation of a stomachless cyprinid, such as northern squawfish, would be described differently than would evacuation in piscivorous fish with stomachs. Steigenberger and Larkin (1974) and Falter (1969) did, in fact, each make conclusions about the evacuation of squawfish which were unusual when compared to work done on evacuation in species with stomachs. Their unusual findings were not, however, consistent with each other's work, nor were they repeated in our study. Our results were generally consistent with work on evacuation of piscivorous fish with stomachs, although some differences were noted.

Our model predicts a rate of increase with temperature that is average for the species reviewed by Durbin and Durbin (1980). Steigenberger and Larkin (1974) reported one of the highest increases, a result of their previously mentioned extremely slow rates at colder temperatures. Our findings also did not support Falter's (1969) unusual conclusion that the evacuation rate in northern squawfish peaks at about 16.5°C.

The effect of predator size on evacuation rates in other species has been inconsistent, but our results are in agreement with several studies done on species with stomachs (Swenson and Smith 1973; Fletcher et al. 1984; and Grove et al. 1985). Apparent disagreement with our results, both in piscivorous fish with stomachs and in the prior studies done on squawfish, could be a result of the effects of prey weight. We found that the influence of prey weight on evacuation is potentially greater than the influence of predator weight. Increases in the ET with increasing predator weight when meal size (% body weight) was held constant (Jobling et al. 1977; Teistlin 1980; Falter 1969) could therefore be caused by the proportional increase in prey weight rather than predator weight. The effect of prey weight could also have contributed to the inconsistent findings of Steigenberger and Larkin (1974) on the effects of squawfish size. They compared size categories of predators which were fed prey which increased slightly in size with increasing predator size.

Our finding that the initial size of a salmon eaten affects its rate of evacuation and emptying time, is consistent with most of the work done on other species with stomachs (Fange and Grove 1979). Our model predicts that both the ER and ET increase as the prey weight increases, in contrast to Steigenberger and Larkin's (1979)

unusual conclusion that the ER decreased as the prey weight increased. Our equation's exponential values of 0.39 and 0.61 for the variable prey weight in the ER and ET equations, respectively, were similar to those derived for other species (Fange and Grove 1979; Jobling 1981).

The nearly constant rate of evacuation over time in our study was compatible with that in other studies on fish, with and without stomachs, in which similar prey (size and type) and methodology was used. By evaluating the relation only up to 90% evacuation, we avoided the slowing of evacuation caused by preferential retention of indigestible parts (Swenson and Smith 1973) and bias introduced by sampling some fish at a time after all food has been emptied from the stomach (Olsen and Mullen 1986). Jobling (1981) determined that large, high energy foods, such as the salmon used in this study, tend to evacuate at a constant rate over time in fish with stomachs. Vondracek (in press) determined that salmon eaten by Sacramento squawfish also evacuated at a linear rate, after an initial period of hydrolysis.

Our results were somewhat unusual in that we did not notice any distinct periods of hydrolysis or lag times before evacuation began. Both Steigenberger and Larkin (1974) and Falter (1969) indicated the presence of lag times. It is possible that lag times in all three of the former studies on squawfish were increased because they force fed prey to the squawfish (Fange and Grove 1979). Studies on fish with stomachs, however, have also reported lag times, which increased with increasing prey size, even when the fish ate voluntarily (Jobling 1986).

Physiological Explanations

Physiological explanations for the influence of prey and predator weight, the linear form of evacuation over time, and the absence of noticeable lag times in our study can only be hypothesized. The explanation for the influence of initial prey weight may be similar to that hypothesized for fish with stomachs. The amount eaten could be directly related to the amplitude of peristaltic contractions and the release of digestive enzymes, thus increasing the mixing of the food with the digestive enzymes and the rate of evacuation (Jobling 1986). Northern squawfish have adapted, in place of a stomach, an enlarged foregut capable of distention and powerful peristaltic contractions. They also have a bile duct, serving both the liver and the pancreas, which enters the tract directly behind the esophagus (Weisel 1962). In other stomachless fish the amount of discharges from the bile duct has been found to be directly related to the amount of food eaten (Chao 1973). Our results indicate that the volume or diameter of

the prey, rather than its surface area, influences the amplitude of contractions and discharges, perhaps through radial distention of the foregut. The exponential value of 0.43 for prey weight in equation 1 is close to 0.5, the value expected if the volume (or diameter) of the prey is directly related to the rate of evacuation (Jobling 1931). Our two-fish experiments also support the idea of a volume dependent rate, at least in the early stages of evacuation, since the two fish, with greater surface area, were not evacuated faster than one-fish meals of similar total weight. The influence of predator weight could be explained by assuming that a larger fish is capable of stronger contractions and a greater amount of discharges.

Increased amplitude of contractions with increasing prey and predator size could also increase the speed with which the food moves through the digestive tract. Our emptying time results indicate that while the speed may increase with predator size, it actually may be reduced with increasing prey size. Hofer et al. (1932) studied the speed with which meal worms and grass moved through the tract of the cyprinid (Rutilus rutilus L.) with continuous feeding, and determined that the speed increased with both the size of predator and the amount consumed per day. It is difficult to know, however, whether the higher consumption caused the food to move faster, or the faster speed made possible the higher consumption.

Although the linear form of evacuation over time was consistent with findings on evacuation in fish with stomachs, the physiological explanation may be different than for fish with stomachs. Jobling (1986) hypothesized an explanation for the fact that the reduced size of the bolus over time did not generally change the rate of evacuation of large, high energy foods in fish with stomachs. His theory could not, however, apply to northern squawfish since it involves a feedback loop between the stomach and the intestine, which depends upon a separating valve and an acid-alkaline cycle. Northern squawfish do not have any separating valve in their digestive tract, nor any gastric glands (Weisel 1962), and cyprinids are generally thought to have entirely alkaline digestion (Al-Hussaini 1949).

We hypothesize another explanation which would be compatible with our model and what is known about squawfish and other stomachless fish. There is evidence that the influence of volume does not last over the entire course of evacuation, since when a strictly constant rate was assumed, as in our Equation 2, the exponent of prey weight was reduced to 0.39. Perhaps as the diameter of the prey decreases over time, the amount of secretions and the amplitude of contractions decrease. The rate may stay nearly constant, however, since the food bolus is at the same time breaking down into pieces which have greater total surface area exposed to the digestive enzymes. Our ET equation, with an exponent

of 0.61 for prey weight, implies that there is a relation between the surface area of the initial prey and the progressive sizes it breaks down into. That exponent is close to 0.67, the value that would be expected if the surface area of the prey was directly related to the emptying time (Fänge and Grove 1979). This theory implies that our equation may not be applicable to multiple meals at the later stages of digestion unless they form a single bolus which later breaks apart similarly to a prey of the same diameter.

The lack of noticeable lag times in our study, as opposed to studies done on fish with stomachs fed large prey, could be explained by an hypothesis of Jobling (1986). He theorized that lags occur because evacuation cannot begin until the stomach breaks down a large prey into pieces which are small enough to pass through the pyloric valve. Since there is no valve prohibiting movement in the squawfish gut and we examined the entire tract, according to his theory we would not expect to find lags.

Conclusions and Recommendations

Our mathematical model furthers our knowledge of the evacuation of salmon in northern squawfish and resolves inconsistencies in prior studies on northern squawfish, but it must still be considered to be only an approximation of evacuation in the natural environment. It is apparently very accurate at predicting results under similar laboratory conditions. It is also applicable to a wide range of water temperatures (10-20°C), prey sizes (4-70 g) and predator sizes (170-1900 g), and can be easily applied to stomach contents from northern squawfish obtained in the field, if the initial prey weight is backcalculated from the length of various bones (Gray et al. 1983). Starvation (up to 96h) before the experiments began could have depressed the ER's (Fänge and Grove 1979), but Falter (1969) observed no significant difference in the rates when squawfish were starved for 48 h. Further studies, perhaps conducted in the field, are needed, however, to determine how sequential feeding affects evacuation and to more extensively study the effects of feeding multiple meals. It would also be useful to investigate the relative rates of evacuation of different size prey eaten in the same meal. Greater understanding of the relation between the model and the underlying physiological processes is not necessary in order to successfully use the model, but it would help in determining the applicability of the model to other conditions and species. We consider our model at this stage to be a useful tool and a base which can be built upon as our knowledge of evacuation in northern squawfish increases. The use of the model will lead to more accurate estimates of consumption of salmon by northern squawfish and will allow managers to determine more precisely the conditions under which maximum consumption occurs.

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REFERENCES

- Brodeur, R.D. 1984. Gastric evacuation rates for two foods in the black rockfish Sebastes melanops Girard. J. Fish Biol. 24: 287-298.
- Durhin, E.G. and A.G. Durbin. 1980. Some factors affecting gastric evacuation rates in fishes. International Council for the Exploration of the Sea, C.M. 1980/L:59. 10 p.
- Elliot, J.M. 1972. Rates of gastric evacuation in brown trout, Salmo trutta L. Reshwatar Biol. 2:1-18.
- Falter, C.M. 1969. Digestive rates and daily rations of northern squawfish in the St. Joe River, Idaho. Ph.D. thesis, University of Idaho, Moscow, ID. 54 p.
- Fange, R. and D. Grove. 1979. Digestion, p. 161-260. In W.S. Hoar, D.J. Randall, and J.R. Bred (ed.) Fish (physiology, volume VIII.) Academic Press, New York, NY.
- Fletcher, D.J., D.J. Grove, R.A. Basimi, and A. Ghaddaf. 1984. Emptying rates of single and double meals of different food quality from the stomach of the dab, Limanda limanda (L.). J. Fish Biol. 25:435-444.
- Gray, G.A. D.E. Palmer, B.L. Hilton, P.J. Connolly, H.C. Hansel, J.M. Beyer and G.M. Sonnevil. 1983. Feeding activity, rate of consumption, daily ration and prey selection of major predators in the John Day Pool. Annual Report to Bonneville Power Administration. Seattle National Fishery Research Center, Cook, WA. 65 p.
- Grove, D.J., M.A. Moctezuma H.R.J. Flett, J.S. Foott, T. Watson, and M.W. Flowerdew. 1985. Gastric emptying and the return of appetite in juvenile turbot, Scophthalmus maximus L., fed on artificial diets. J. Fish Biol. 26:339-354.

- Jobling, M. 1980. Gastric evacuation in plaice, Pleuronectes platessa L.: effects of dietary energy level and food consumption. J. Fish Biol. 17:187-196.
- Jobling, M. 1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. J. Fish Biol. 19:245-257.
- Jobling, M., D. Gwyther, and D.J. Grove. 1977. Some effects of temperature, meal size and body weight on gastric evacuation time in the dab, Limanda limanda (L). J. Fish Biol. 10:291-298.
- Macdonald, J.S., K.G. Waiwood, and R.H. Green. 1982. Rates of digestion of different prey in Atlantic cod (Gadus morhua), ocean pout (Macrozoarces americanus), winter flounder (Pseudopleuronectes americanus), and American plaice (Hippoglossoides platessoides). Can. J. Fish. Aquat. Sci. 39:651-659.
- Medved, R.J. 1985. Gastric evacuation in the sandbar shark, Carcharhinus plumbeus. J. Fish Biol. 26:239-253.
- Molnar, Gy., E. Tamassy, and I. Tolg, 1967. The gastric digestion of living predator fish, p. 151-173. In S.D. Gerking (ed.) The biological basis of freshwater fish Blackwell Scientific Publications. Oxford, England.
- Neter J., W. Wasserman, and M.H. Kutner. 1983. Applied linear regression models. Richard D. Irwin, Inc., Homewood, IL. 545 p.
- Olso, R.J., and A.J. Mullen. 1986. Recent developments for making gastric evacuation and daily ration determinations. Environ. Biol. Fishes. 15:183-191.
- SAS Institute Inc. 1985. SAS User's Guide: Statistics, Version 5 Edition. SAS Institute Inc., Cary, NC. 956 p.
- Steigenberger, L.W., and P.A. Larkin. 1974. Feeding activity and rates of digestion of northern squawfish (Ptychocheilus oregonensis). J. Fish. Res. Board Can. 31:411-420.

- Swenson, W.A., and L.L. Smith Jr. 1973. Gastric digestion and food consumption, feeding periodicity, and food conversion efficiency in walleye (Stizostedion vitreum vitreum). J. Fish. Res. Board Can. 30:1327-1336.
- Tseitlin, V.B. 1980. Duration of gastric digestion in fishes. Mar. Ecol. 2: 277-280.
- Uremovich, B.L., S.P. Cramer, C.F. Willis, and C.O. Junge. 1980. Passage of juvenile salmonids through the ice-trash sluiceway and squawfish predation at Bonneville Dam, 1980. Annual Report to U.S. Army Corps of Engineers DACW57-78-C-0058. Oregon Department of Fish and Wildlife. 46 p.
- Windell, J.T. 1966. Rate of digestion in the bluegill sunfish. Invest. Indiana Lakes Streams 7:185-214.
- Zar, Jerrold H. 1984. Biostatistical analysis Second Edition. Prentice-Hall, Inc., Englewood Cliffs, NJ. 478 p.

Gastric Evacuation in Smallmouth bass (Micropterus dolomieu)

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ABSTRACT

Laboratory experiments were conducted to examine the effects of water temperature (10, 15, 20°C), predator size (29 - 1550g), prey size (0.20 - 5.0g) and prey number (1-3) on gastric evacuation of juvenile salmon in smallmouth bass (Hicropterus dolomieui). The bass were allowed to feed voluntarily and their stomachs pumped at 1-4h intervals until 1 evacuation approximated 90%. The rate of evacuation increased with increases in all the variables examined = meal weight, time, temperature, predator weight, and prey number (listed in order of decreasing importance). The 90% emptying times increased with increasing prey weight, and decreased with increasing temperature, predator weight, and prey number. The emptying times over the range of the variables tested were approximately 3-78h.

INTRODUCTION

Reliable estimates of the amount of juvenile salmon consumed by smallmouth bass (Micropterus dolomieu) have not been possible in the past because knowledge of smallmouth bass gastric evacuation rates under varying conditions was not available. Several studies have indicated that smallmouth bass do consume outmigrating salmon (Warner 1972, Pflug and Pauley 1983, Grey et al. 1984, Grey and Rondorf 1986). Pflug and Pauley (1983) found that during periods of peak outmigration, salmonids are the major prey item of smallmouth bass in Lake Sammamish, Washington. Lane and Jackson (1969) did test the voidance time (the time it took to pass all food from the fish) of daphnia and fish fry in 0.3-1.3g smallmouth bass at 12°C, but their results may not be applicable to bass in the size range that eat salmon, to salmon prey, nor to predation under other water temperatures. Factors that may affect gastric evacuation include predator size (Swenson and Smith 1973; Jobling et al. 1977), size and type of meal (reviewed by Fänge and Grove 1979), and water temperature (Molnar et al. 1967; reviewed by Durbin and Durbin 1980).

Several studies have been done on adult largemouth bass, (Micropterus salmoides) (Markus 1932; Hunt 1960; Molnar and Tolg 1962; Beamish 1972; Lewis et al. 1974; Adams et al. 1982; and Perez et al. 1985), and while it is possible that their evacuation rates may be applicable to smallmouth bass, this can not be assumed. The two species are members of the same genus, with similar diets (Lewis and Helms 1964), and Lane and Jackson (1969) did find that in fingerling bass evacuation times are similar (48-72h for smallmouth bass compared to 48-84h for largemouth bass). Smallmouth bass do, however, prefer colder (Ferguson 1958; Scott and Crossman 1973) and faster moving water (McClane 1974) suggesting that they have different metabolisms and thus different evacuation rates.

Evacuation rates of smallmouth bass can be used not only to estimate consumption of juvenile salmonids, but also to assess that consumption relative to the other predators of salmonids, such as the northern squawfish (Ptychocheilus oregonensis). Efforts are presently being made, to determine the consumption rates of the resident predators in a reservoir of the Columbia River (USA) (Poe et al. 1988). Comparison of evacuation rates and resulting consumption rates is facilitated if the same information is available on both species, so an attempt was made in this study to employ experimental design and data analysis methodology similar to that used previously for northern squawfish (Beyer et al. 1988).

The specific objectives of our study were to determine the rates of evacuation of juvenile salmon in smallmouth bass under varying water temperatures, prey weights, predator weights, and prey numbers, and to express the rates in a single, easily applied equation.

METHODS

Smallmouth bass gastric evacuation experiments were conducted using an experimental design similar to that used by (Beyer et al. 1988) for northern squawfish, testing three water temperatures, prey size groups, and predator size groups. The smallmouth bass were collected during May 1985-August 1986, from the John Day Reservoir, Columbia River and John Day River, Oregon and divided into groups <200mm, 200-300mm, and >300mm. The bass were acclimated to water temperature (10°C, 15°C, or 20°C) and a 12h photoperiod over a period of two weeks. Prior to tests, the fish were starved 24-48h to empty the stomachs (based on preliminary trials). The smallmouth bass were used more than once, with a minimum of seven days between tests. The juvenile salmon prey fish were obtained from the Little White Salmon and Willard National Fish Hatcheries, Cook, Washington and were divided into three groups: 0.26-0.38g, 1.0-1.8g, and 3.0-5.0g.

Experiments were conducted similarly to Beyer et al. (1988), except that up to three prey in the selected size group were presented to the smallmouth bass and the prey remains were obtained by stomach pumping. Prior to use in the experiments, the salmon were weighed (+0.001g) and marked with color-coded threads sewn between the dorsal fin and backbone. The prey were made available to each section of predators during the first hour of light and checked at one-half hour intervals, with time of ingestion recorded at the midpoint of the interval in which feeding occurred. As soon as at least one of the prey in a section was eaten, the remainder in that section were removed. After the predetermined time (1-4h intervals until evacuation approximated 90%), the predators in a section were anesthetized using Tricaine Methane Sulfonate (MS-222), and weighed to the nearest gram. Stomach pumping of the bass was continued until all the eaten prey were recovered (evidenced by obtaining the color-coded threads). The pump consisted of a modification of the stomach sampler developed by Seaburg (1957). A single 0.64cm copper tube was soldered to a threaded garden hose attachment and attached to a trigger action spray nozzle; water was pumped from a reservoir tank by a 12 volt bilge pump. Each fish stomach was flushed with water at $1.9 \text{ l} \cdot \text{min}^{-1}$ into a holding bucket. Flushing was continued until all food items had been removed and approximately 30s had elapsed without any food items being removed. The water and food material were strained in a 333µm sieve to obtain the samples. The samples were weighed (+ 0.001g) after preservation in formalin for at least 2 weeks. Emphasis was on obtaining at least five single meal samples at each interval tested, with multiple meals obtained when the smallmouth bass ate more than one prey.

The data were analyzed using similar methodology to that used on the single meal northern squawfish data (Beyer et al. 1988), employing SAS statistical programs (SAS Institute Inc. 1985). In addition to examining the effects of time, meal weight, temperature, and predator weight, the effect of increasing the number of prey in a meal was tested by including it as a possible independent variable.

Some of the samples had weights which exceeded the initial meal weight, so in those cases the amount evacuated was assumed to be zero. Since the logarithmic transformation could not be performed with zero values, several methods of performing that transformation were compared. These included adding 0.01g or 0.0001g to all the grams evacuated before transformation, or replacing the zero values with 0.0001g.

RESULTS

All of the independent variables tested were selected in the chosen logarithmic model (Table 1). Those variables were meal weight, time, temperature, predator weight, and number of prey (with logarithmic transformations of meal, time, and temperature), listed in the order they were selected using the Cp criteria. The addition of number of prey improved both the mean square residual (MSR) and the bias, since it reduced the Cp value from 13 to 6, and made it closer to the number of variables selected. In the linear and square root models, however, the number of prey did not improve either factor and was therefore not included as a variable (Table 1). The correlation between the independent variables was highest for temperature and time ($r=-0.48$). Meal weight and number of prey had a correlation of 0.40, but this was reduced to 0.25 when the logarithmic transformation was applied to meal weight. There was a very slight correlation between meal weight and predator weight ($r=0.10$), since the small predators were able to eat even the largest prey (Table 2). The meal sizes eaten ranged from 0.04-12.90 percent body weight, with an average of 1.96 percent.

The model selected was considered to best fit the data and meet the necessary assumptions, but several of the models were very close in those aspects. The linear and square root models had slightly lower MSR values than the selected model (Table 1). Examination of the residuals also indicated that the square root model was slightly better than the selected model at producing homogeneity of variance, since the log transformation tended to overcompensate for the heteroskedasticity. The residuals also indicated, however, that the log transformation was the model best able to fit the curvilinear relation between grams evacuated and time. The selected model was better at showing the

Table 1. Comparison of equations expressing gastric evacuation in smallmouth bass (sample size = 580).

Model	R^2	MSR	Intercept	Coefficients				
				Time(h)	Meal(g)	Temp(°C)	Predator(q)	#prey
Evacuation (q)								
Linear	0.73	0.36	-2.495	0.099	0.239	0.120	0.0008	
Squarefoot	0.79	0.36	-1.092	0.057	0.105	0.071	0.0003	
Exponential^b	0.68	8.05	-6.886	0.175	0.201	0.231	0.001	0.156
Log-Log ^b	0.80	0.40	-14.914	1.740^a	0.385^a	3.364^a	0.276^a	0.321^a
	ⁱ 0.80	0.37	-9.718	1.754^a	0.385^a	0.238	0.277^a	0.197

^a = logarithmic transformation

^b = Evacuation (q) + 0001

ⁱ = selected model

Table 2. Sample size, and means of meal size (g) and predator weight (g), stratified by temperature, prey size group (g), and prey number.

		Small prey group 0.33 g (0.26-0.38 g)			Medium prey group 1.5 g (1.0-1.8 g)			Large prey group 3.7 g (3.0-5.0 g)		
# prey	Temp	Sample size	Meal weight	Predator weight	Sample size	Meal weight	Predator weight	Sample size	Meal weight	Predator weight
1	10	31	0.34	186	51	1.46	244	63	3.74	266
	15	42	0.32	205	58	1.40	252	84	3.68	284
	20	38	0.32	195	41	1.59	283	61	3.70	177
2	10	6	0.65	116	7	2.95	396	13	7.35	240
	15	4	0.63	174	20	2.86	160	11	7.48	389
	20	12	0.63	170	5	2.99	104	10	7.43	187
3	10	1	1.09	233	4	4.32	407	0	---	---
	15	0	---	---	4	4.42	290	4	11.39	426
	20	7	0.93	124	1	5.31	199	2	11.23	124
Predator Size		Grams: 187 (33-752)			252 (29-1526)			253 (29-1550)		
		216 Millimeters: (117-458)			235 (128-455)			234 (129-460)		

initial lag times before evacuation began and it did not result in predictions of negative time, as the linear model did, or decreases in grams evacuated with time, as the square root model did, given certain values for the independent variables. The models with the dependent variable expressed as percent remaining produced consistently lower R^2 values than the grams evacuated models, and the logarithmic models which used 0.0001 had lower MSR than adding 0.01 to the grams evacuated.

The model chosen, expressed in exponential form, was

$$E + 0.01 = 0.00006 S^{0.385} t^{1.754} e^{0.238T} w^{0.277} e^{0.197N},$$

$$R^2=0.80, n=580$$

where E=mass evacuated (g), S=meal weight (g), t=time (h), T=temperature (°C), W=predator weight (g), and N=prey number. This model indicates that the rate of evacuation increased with increasing time, meal weight, temperature, and predator weight, and number of prey; while the 90% emptying times increased with meal weight and decreased with increasing temperature, predator weight and prey number. The 90% emptying times approximately doubled when the meal weight increased 10 times, and decreased by about three-fourths when the temperature doubled (Figure 1). Increasing predator weight 10 times reduced the emptying time by about one-third and increasing the prey number from one to three decreased the time by about one-fifth. Ninety percent evacuation times over the range of the data (Table 2) was 3h for a 0.26g salmon, 1550g bass at 20°C to 78h for a 12.04g meal, a 29g bass, at 10°C.

DISCUSSION

Comparison with Largemouth Bass

Our results indicate that emptying times of salmon in smallmouth bass are faster than would be estimated using most of the comparable largemouth bass evacuation studies; application of those largemouth bass emptying times to smallmouth bass data may underestimate the consumption of salmon. Under similar water temperatures, prey sizes, and predator sizes, our equation predicts emptying times 1-118h faster (0-115h if 100% evacuation is extrapolated using our equation) than the largemouth bass studies which were within the range of the variables we tested (Markus 1932; Lewis et al. 1974; and Adams et al. 1982) (Table 3). Molnar and Tolg's (1962) study was conducted at similar water temperatures, but could not be directly compared since they reported prey and predator size in lengths rather than weights (Table 3).

Methodology could be responsible for at least part of the difference in times, as evidenced by the study most resembling ours in

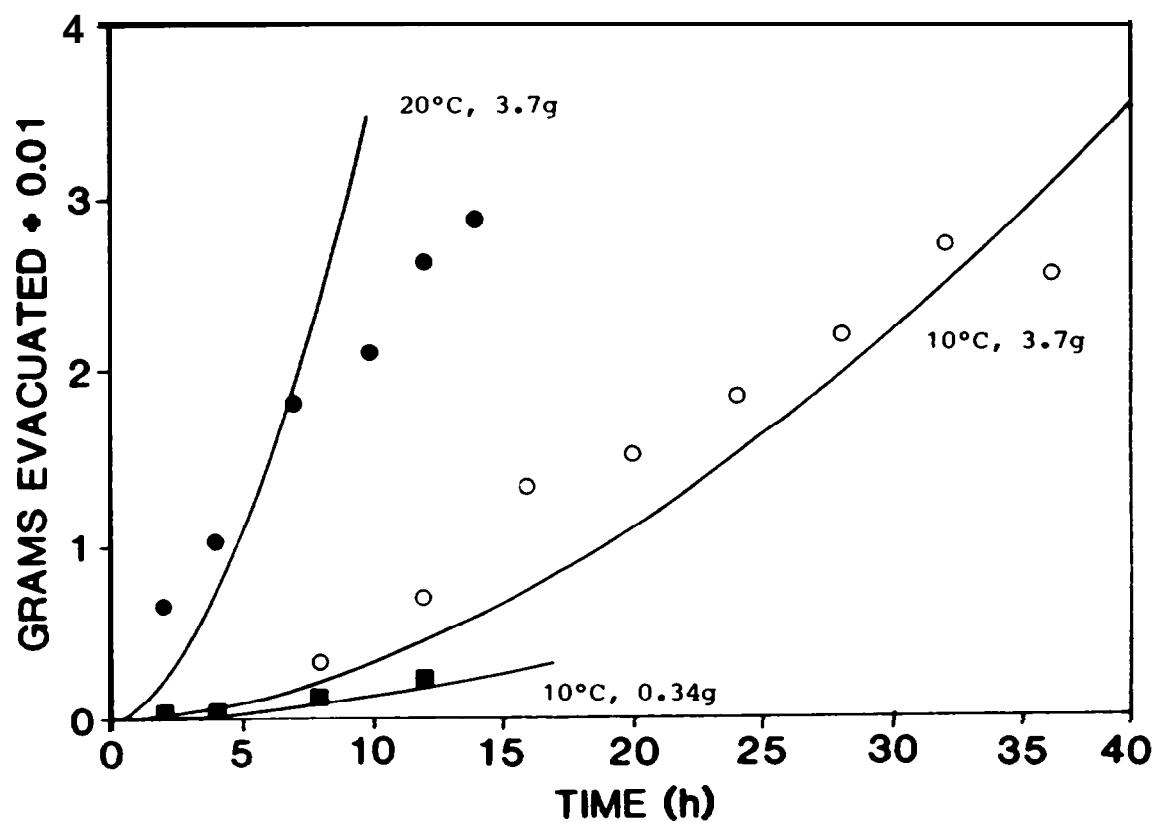


Figure 1. Comparison of the effects of increasing the water temperature 2 times and the prey weight 10 times on evacuation rates in smallmouth bass. The endpoint of each line is to 90 percent emptying time (symbols = means of 3 - 11 samples).

Table 3. Comparison of predicted largemouth bass emptying times to our smallmouth bass 90% predicted emptying times at the same water temperatures, predator sizes, and prey sizes.

Temperature °C	(% Evac.) time (h)	# Hours Slower than ours	Sample Size	Fish Size(g)	Prey Size(g)	Prey Type	*Method	Reference
(100%)								
10	168	116,118	2	33,39	4	minnow	1B	Markus (1932)
	92	46,48	2	121,158	5			
16	84	61,62	2	30,39	4			
	32	12,13	2	123,160	5			
10	50	+	10	25-27cm	8-8.5cm	bleak	4B	Molnar and Tolg(1962)
15	37	+	10					
20	24	+	10					
18	30	9-15	30	200-400	3.0- 4.1% minnow	gizzard shad	2B	Lewis et al.(1974)
(95%)								
14	27	1-3	<30	400-700	2 % ration	fathead minnow	3A	Adams et al.119821
17	24	5-7	<30					
20	18	6-7	<30					

I Methods: (1) Injection of HCl into stomach to cause regurgitation (2) Fish sacrificed and stomach contents removed (3) Stomach pumped (4) x-ray analysis at time intervals: (A) Voluntary feeding (B) Force feeding.

+Information not available

methodology (Adams et al. 1982) reporting the most similar times (Table 3). The slower times in all the studies could be partially a result of their approximating emptying times up to 95% (Adams et al. 1982) or 100% (Markus 1932; Lewis et al. 1974), thereby reflecting the slow passage of indigestible hard parts in the last 10% of evacuation (Karpevitch and Bakoff 1937) and/or sampling some fish after the time of 100% evacuation (Olsen and Mullen 1986). In addition, all the largemouth bass studies compared used non-salmonid prey (Table 3), so the difference in prey species could be a factor in the slower times. Markus (1932) and Lewis et al. (1974) also force fed the prey to the largemouth bass, which can slow the digestive processes of the fish (Windell 1966; Swenson and Smith 1973) and used methods other than stomach pumping to empty the stomachs (Table 3).

There was not sufficient information available to determine whether or not the differences between species was related to water temperature or predator size. Comparing our study to that of Markus (1932) indicated that the difference between largemouth bass and smallmouth bass emptying times may decrease as water temperature and predator weight increases. Methodology could not be responsible for the change in differences since he applied the same methods to all his fish. Since his sample sizes were so small (Table 3), however, his results cannot be considered conclusive. His results at temperatures outside our study's range (4°C and 22°C) did not show his same large change in largemouth bass emptying times with increasing predator weight, and the results of Adams et al. (1982), though conducted at a higher water temperature range, indicated the difference between species did not change substantially (and if anything increased) with increasing temperature (Table 3).

Comparison with Northern Squawfish

Comparing our equation to the similar equation derived for the stomachless northern squawfish (Ptychocheilus oregonensis) (Beyer et al. 1988) shows several differences. The smallmouth bass equation indicates longer lag times before evacuation begins (the exponent for time is 1.74 compared to 0.93 for squawfish). The longer lag times could be attributed to both differences in physiology and technique. Smallmouth bass have stomachs which were pumped, while northern squawfish are stomachless and the entire tract was removed. Jobling (1986) hypothesized that lags occur in fish with stomachs because evacuation from the stomachs cannot begin until a large prey is broken down into pieces which are small enough to pass through the pyloric valve.

Other differences between the equations are that evacuation rates under comparable conditions for smallmouth bass are slower, but show a greater increase when the temperature is raised from 10-20°C. Under

similar conditions (5g salmon and 700g bass), the bass equation predicts 90% emptying times of 35h at 10°C and 4h at 20°C. This indicates that squawfish have the potential of being greater predators on salmon than smallmouth bass, particularly at colder temperatures, since they could eat more salmon in a given time period. The difference in the change with temperature could be attributed to a difference in temperature preference. Northern squawfish prefer water more within the range tested, 16-22°C (Brown and Moyle 1982), while smallmouth bass prefer temperatures up to 27°C (Sigler 1982, Ferouson 1958, McLane 19741, and show reduced activity and feeding at 10°C (Scott and Crossman 1973).

According to the model we selected, the number of prey in a meal affects the evacuation rate, while no effect was found in the squawfish investigation of prey number at 4h evacuation time. An increase in rate with increase in prey number, as indicated by the smallmouth bass logarithmic models, could be attributed to the accompanying increase in the total surface area available to the digestive juices, or to shorter lag times if multiple prey break down into smaller pieces faster, as hypothesized by Beyer et al. (1988). The difference between species could be because the surface area of the prey may have more effect in a fish with a stomach, since more through mixing may be possible, particularly in the initial stages of evacuation. In the squawfish study, the multiple prey were found very tightly packed into the anterior limb of the digestive tract (J. Beyer, personal observations). The difference in results could also possibly be attributed to the fact that the squawfish results were based only on the initial stage of evacuation (4 h) and the smallmouth bass results covered all stages of evacuation. The equations derived in the squawfish study did indicate the possibility that volume had more influence at the start of evacuation and surface area more influence in the later stages (Beyer et al. 1988).

Conclusions

Our equation makes possible more reliable estimates of smallmouth bass consumption of salmon. Development of a new model which fit the data better than any of the models we tested would make the choice of a model more definitive, and further increase the accuracy of the consumption estimates. Such a model would have to both approximate the s-shaped curve of evacuation over time and produce homogeneity of variance. More extensive multiple meal experiments could resolve the discrepancy regarding the effect of prey number in the models we tested. Further studies in which evacuation in the field is examined would be beneficial in assessing the applicability of our model to predation under natural conditions.

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References

- Adams, S.M., R.B. McLean, and M.M. Huffman. 1982. Structuring of a predator population through temperature-mediated effects on prey availability. *Can. J. Fish. Aquat. Sci.* 39: 1175-1184.
- Beamish, F.W.H. 1972. Ration size and digestion in largemouth bass, Micropterus salmoides Lacepede. *Can. J. Zool.* 50: 153-164.
- Beyer, J.J., G. Lucchetti, and G. Gray. 1988. Digestive tract evacuation in northern squawfish (Ptychocheilus oregonensis). *Can. J. Fish. Aquat. Sci.* 45: 548-553.
- Brown, L.R. and P.B. Moyle. 1982. The impact of squawfish on salmonid populations: a review. *N. Am. J. Fish. Manage.* 1:104-111.
- Durhin, E.G., and A.G. Durbin. 1980. Some factors affecting gastric evacuation rates in fishes. *Int. Conc. Explor. Sea, C.M.* 1980 L:59:10p.
- Fänge R., and D. Grove. 1979. Digestion, p. 161-260. In W.S. Hoar, D.J. Randall, and J.R. Brett (ed.) *Fish physiology*. Vol. VIII. Academic Press, New York, N.Y.
- Ferguson, R.G. 1958. The preferred temperature of fish and their mid summer distribution in temperate lakes and streams. *J. Fish. Res. Bd. Can.* 15: 607-624.
- Grey, G.A. and D.W. Rondorf. 1986. Predation on Juvenile Salmonids in Columbia Basin Reservoirs. *Reservoir Fisheries Management Strategies for the 80's*. Reservoir Committee, South division American Fisheries Society, Bethesda, Maryland. pp. 178-185.
- Grey, G.A., G.M. Sonnevill, H.C. Hansel, C.W. Huntington, and D.E. Palmer. 1984. Feeding activity, rate of consumption, daily ration and prey selection of major predators in the John Day Reservoir. Report to the Bonneville Power Administration, United States Fish and Wildlife Service, National Fisheries Research Center, Cook, Washington, USA.

- Hunt, B.P. 1960. Digestion rate and food consumption of Florida gar, warmouth, and largemouth bass. Trans. Amer. Fish. Soc. 89: 206-210.
- Jobling, M., D.Gwyther and D.J. Grove. 1977. Some effects of temperature, meal size and body weight on gastric evacuation time in the lab Limanda limanda (L.) J. Fish. Biol. 10: 291-298.
- Jobling, M. 1986. Mythical models of gastric emptying and implications for food consumption studies. Environ. Biol. Fishes 16: 35-50.
- Lane, T.H. and H.M. Jackson. 1969. Voidance time for 23 species of fish. Investigations In Fish Control 33. United States Department of the Interior. Washington, D.C. 9 p.
- Karpevitch, A., and E. Bakoff. 1937. The rate of digestions in marine fishes. Zool Zh. 16: 28-44.
- Lewis, W.M., R. Heidinger, W. Kirk, W. Chapman, and D. Johnson. 1974. Food intake of the largemouth bass. Trans. Amer. Fish. Soc. 103: 277-280.
- Lewis, W.M. and D.R. Helms. 1964. Vulnerability of forage organisms to largemouth bass. Trans. Amer. Fish Soc. 93: 315-318.
- Markus, H.C. 1932. The extent to which temperature changes influence food consumption in largemouth bass (Huro floridana). Trans. Amer. Fish. Soc. 115: 314-321.
- McClane, A.J. 1974. McLane's field guide to freshwater fishes of North America. Holt, Rinehart and Winston, New York 212 p.
- Molnar, G.Y., E. Tamassy, and I. Tolg. 1967. The gastric digestion of living predatory fish, p 151-173. In S.D. Gerking (ed.) The biological basis of freshwater fish Blackwell Scientific Publications, Oxford, England.
- Molnar, G.Y., and Tolg, F. 1962. Relation between water temperature and gastric digestion of largemouth bass Micropterus salmoides Lacepede. J. Fish. Res. Bd. Can. 19: 1005-1012.

- Olsen, R.J., and A.J. Mullen. 1986. Recent developments for making gastric evacuation and daily ration determinations. Environ. Biol. Fishes 16: 183-191.
- Perez, A.M., F.P. Guerra, and M. Penaz. 1985. Feeding habits of Micropterus salmoides in Cuba. Acta. Sc. Nat. Brno. 19: 1-36.
- Pflug, D.E., and G.B. Pauley. 1983. Biology of smallmouth bass (Micropterus dolomieu) in Lake Sammamish, Washington. N.W. Sci. 58: 118-130.
- Poe, T.P., H.C. Hansel, S. Vigg, D.E. Palmer, and L.A. Prendergast. 1988. Predation by northern squawfish, walleye, smallmouth bass, and channel catfish in a mainstem Columbia River reservoir: I. Feeding ecology during the salmonid smolt out-migration. MS in preparation.
- SAS Institute Inc. SAS/STAT Guide for Personal Computers, Version 6 Edition. Cary, NC: SAS Institute Inc., 1985. 378 pp.
- Seaburg, K.G. 1957. A stomach sampler for live fish. Prog. Fish Cult. 19: 137-139.
- Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of North America. Holt, Rinehart and Winston, New York. pp. 212.
- Sigler, W.P. and J.W. Sigler. 1987. Fishes of the great basin a natural history. Max C. Fleischmann series in great basin natural history. University of Nevada Press. 425 p.
- Swenson, W.A., and L.L. Smith Jr. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (Stizostedion vitreum vitreum). J. Fish. Res. Board Can. 30: 1327-1336.
- Warner, K. 1972. Further studies of fish predation of salmon stocked in Maine lakes. Prog. Fish Cult. 34: 217-221.
- Windell, J.T. 1966. Rate of Digestion in the Bluegill Sunfish. Invest. Indiana Lakes & Streams, Vo. VII, No. 6. pp. 185-214.

Feasibility of Reducing or Controlling Predation Induced Mortality
of Juvenile Salmonids in Columbia River Reservoirs

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INTRODUCTION

A recent study was conducted in John Day Reservoir of the Columbia River to determine the significance of predator-induced mortality on outmigrating juvenile salmonids (Poe et al. 1988, Vigq et al. 1988, Beamesderfer and Rieman 1988, and Rieman et al. 1988); results of this study indicate that predation by resident fish predators can easily account for previously unexplained mortality of juvenile salmonids during their seaward migration (Rieman et al. 1988). The reduction of the mortality of outmigrating juvenile salmonids is a high priority goal of the Northwest Power Planning Council's Fish and Wildlife Plan (1987) because this mortality may be one of the major impediments in the restoring Columbia River anadromous salmonid runs. Reduction or control of predation-induced mortality on juvenile salmonids may significantly reduce overall mortality.

We therefore conducted a preliminary evaluation to determine the feasibility of regulating predation on juvenile salmonids by major predators by: (1) identifying and describing potential predation control measures from the literature, (2) evaluating the biological feasibility of predation control measures and, (3) identifying additional information needs. The results of the preliminary evaluation are reported in this paper.

We considered control measures that decrease the size of predator populations (predator control) or reduce the susceptibility of juvenile salmonids to predation (prey protection). Our evaluation of control measures was limited to biological feasibility because the social and economic considerations, although exceedingly important, cannot be fully addressed until after the magnitude of predation-induced mortality has been more clearly delineated and the list of potential control measures reduced to those most feasible. Throughout this paper we emphasized northern squawfish Ptychocheilus oregonensis, as the primary target for predation control and prey protection measures because Rieman et al. (1988) reported that northern squawfish were responsible for the majority (~ 78%) of juvenile salmonid losses to predators.

The first objective of this study, the literature review, has already been completed and reported in a U.S. Fish and Wildlife Service Annual Report (1984) to BPA (Gray et al. 1986). That report not only presented a literature review of previous attempts to control or reduce predation but also discussed the pros and cons of each predation control measure and its possible application to Columbia River reservoirs.

METHODS

Criteria used to evaluate potential measures to reduce losses of juvenile salmonids by predation were: (1) demonstrated success, (2) applicability, (3) selectivity, (4) side effects, and (5) timeliness. To meet the first criterion, demonstrated success, a measure must have been used successfully in a majority of the fisheries field applications that we reviewed. To meet the second criterion, applicability, a measure must have been used or we judged it could be used effectively in a system of the type (i.e. cool water river with extensive network of dams) and size as the Columbia River. To meet the third criterion, selectivity, a measure must have been used or we judged it could be used to control any of the four major predators in the system (northern squawfish, walleye, smallmouth bass, and channel catfish) without having significant impact on other fish species in the Columbia River. To meet the fourth criterion, absence of side effects, a measure must not cause significant adverse environmental impacts (impacts on water quality, benthic invertebrates, etc.) when used. To meet the fifth criterion, timeliness, a measure must be suitable for implementation within no more than two years and take no longer than four years to see a measurable effect (a six year maximum). We considered a measure to have high potential for reducing predation of juvenile salmonids if it met at least four of the five criteria, moderate potential if it met two or three of the above criteria, and low potential if it met fewer than two of the above criteria. We also rated a measure as having low potential if it had a side effect which was unacceptable even though it met all other criteria (e.g. a pathogen would not be acceptable to use even if it met all criteria but caused adverse effects on benthic invertebrates in the system).

RESULTS AND DISCUSSION

We evaluated 11 predation control measures and 12 prey protection measures for reducing predation on juvenile salmonids in the Columbia River reservoirs (Table 1). There were often insufficient data available to rate many of the measures for certain criteria, therefore additional research and testing of many of these measures would be needed before a final evaluation can be made. We rated two predator control measures (netting/trapping and harvest regulations) and five prey protection measures (dam lighting, release sites, release times, release number, and bypass location) as having high potential (Table 1) and discuss each of these measures below.

Netting and Trapping Netting and trapping have been used to reduce abundance of undesirable fish, including predators. Past efforts met with various degrees of success and were often deemed effective

Table 1. Evaluation of predation control measures based on their potential to reduce predation on juvenile salmonids in the Columbia River reservoirs.

Measure	Criteria					Potential ²
	Demonstrated success	Applicability	Selectivity	Absence of side effects	Timeliness	
<u>Predator Control</u>						
Netting & trapping	+ ¹	+	+	+	I	High
Electrofishing	0	I	+	+	I	Moderate
Explosives	+	0	0	I	I	Low
Harvest regulations	I	+	+	+	+	High
Water level manipulations	+	+	I	I	0	Moderate
Squoxin	+	I	+	I	0	Low
Antimycin	+	+	0	0	+	Low
Rotenone	+	0	0	0	+	Low
Sterilization	I	I	+	+	0	Moderate
Predator introduction	I	+	0	0	0	Low
Pathogen introduction	I	+	I	0	I	Low
<u>Prey Protection</u>						
Dam lighting	I	+	+	+	+	High
Release sites	I	+	+	+	+	High
Release times	I	+	+	+	+	High
Release number	I	+	+	+	+	High
Smolt bypass location	I	+	+	+	+	High
Electrical barriers	I	+	0	I	I	Low
Bubble barriers	0	+	0	I	I	Low
Hydro-acoustics	0	+	0	I	I	Low
Predator attractants	I	+	+	+	0	Moderate
Predator repellents	I	+	+	+	0	Moderate
Alternate prey introduction	I	+	0	0	I	Low
Predator-avoidance conditioning	I	+	+	+	I	Low

¹ + = Met criterion
 0 = Did not meet criterion
 I = Insufficient information to rate measure.

² High = Met 4 or 5 criteria
 Moderate = Met 2 or 3 criteria
 Low = Met 0 or 1 criteria or measure would have side effect(s) which is unacceptable even though all other criteria were met.

(Table 2). Many studies, however, have failed to conduct post-removal evaluations to determine if removal efforts changed the population structure of the targeted species and if the change persisted through time.

Netting and trapping may be better than chemical and biological treatments for some systems because it is relatively inexpensive, allows better selection of size and species removed, has known effect on mortality of non-target species, can produce benefits (an improved fishery) in a relatively short time, and can be accomplished with non-technical assistance (Hanson et al. 1983). Removal by netting and trapping also has little or no impact on the abiotic environment; although McCrimmon (1968) suggested that seines be used with caution because they scour the bottom fauna and could denude sport fish habitat, especially spawning areas.

The primary limitation of netting and trapping is that it depends largely upon vulnerability of the target species and effort expended. Except in backwaters and other protected areas, netting and trapping in the relatively swift-flowing Columbia River reservoirs would likely have limited application particularly in highly turbulent tailwaters below dams where predators often concentrate. Seasonal movements of walleye and northern squawfish out of areas accessible to nets and traps presently make these species difficult to locate at times.

Sport and Commercial Harvest Use of sport and commercial fisheries to reduce fish predation is not well documented. Fisheries have traditionally been regulated to allocate and conserve fish resources. Harvest is often regulated by size limits, catch limits, and restricted fishing seasons. Since sport fisheries on the target species are presently open all year, we will not discuss effects of restricted fishing seasons on predator populations. None of the target predator species is currently being harvested commercially.

Size limits are commonly used in sport fisheries management to protect a segment of the population (e.g. spawners or young fish), maximize fishing yield, and prevent overharvest. Minimum size limits are generally used to protect young fish (Table 3) and allow a greater proportion of the population to grow to a larger size. Removing size limits should cause a shift in age structure because of increased exploitation of smaller fish. This could affect the reproductive potential of the population by reducing the number of times the average fish spawns and the number of females that will survive to larger, more fecund egg producers.

Creel limits reduce the average daily harvest (Allen 1955) and are usually enacted to conserve potential spawning stock and allocate harvest equitably among anglers.

Table 2. Summary data from studies on the effectiveness of netting and trapping as a control measure.

Measure	Duration of effort (yrs)	Type of system & size (ha)	Target species ¹	Results	Reference
Trapnets, hoopnets, and trawls	11	lake 55,730	freshwater drum	-decrease in the average age of drum -did not reduce gamefish populations -some gamefish populations increased	Priegel 1971
Seining and trapping (intensive)	12	lake 567	bigmouth buffalo, carp, freshwater drum	-decline in target fish -increase in game fish	Rose & Moen 1952
Fyke nets	5	ponds & lakes 9-109	mostly centrarchids, yellow perch white perch	-species removed showed increased growth rates -number of large gamefish did not increase	Grice 1958
Gillnetting, dynamiting, reservoir fluctuation, and rotenone	6	Hayden lake 1540	northern squawfish	-24,000 lbs. of northern squawfish removed -catches of predators declined 90% over the length of the experiment -improved fishing for salmonids	Jeppson & Platts 1959

Table 2. (continued)

Measure	Duration of effort (yrs)	Type of system & size (ha)	Target species ¹	Results	Reference
Gillnetting and seining	6	Cultus Lake 626	northern squawfish & Arctic char	-decrease of northern squawfish and Arctic char to 10% previous levels -young sockeye salmon 2 1/2 to 4 1/2 times greater survival	Foerster & Ricker 1941
Confinement of fish	1	4 large lakes interconnected by swift streams, Wood River system	Arctic char	-estimated 900,000 smolts saved	Meacham & Clark 1979
Gillnets, trammel nets, hoop nets, angling, and poison chemicals	15	Heming Lake, <1	northern pike	-number of northern pike was reduced -main emphasis: disrupt life cycle of a parasite infecting lake whitefish -little angling done -initial chemical attempts considered futile	Lawler 1965
Fyke nets	1	English Lake 20	black crappie black bullhead	-removal of large numbers of small blackcrappie and black bullhead increased growth rates for these same species	Hanson et al. 1983

¹ Common names are used here and throughout the remainder of the report, and the scientific names for each species mentioned may be found in Appendix II E.

Table 3. Selected examples of studies where alteration of fishing regulations was used as a control measure.

Measure	Area & Location	Target Species	Results	Reference
Minimum size limit (305 mm)	Pony Express Lake, Missouri	largemouth bass	accumulation of slow-growing sublegal fish	Ming & McDannold 1975
Minimum size limit (381 mm)	Big Crooked Lake, Wisconsin	walleye	-four-fold decrease in yield (kg/hectare) and angler catch of legal fish first four years -number of sublegal walleyes increased -growth, condition factor, mean length and weight of angled walleye declined	Serns 1978
Minimum size limit (559 mm)	Escabana Lake, Wisconsin	northern pike	number of fish increased by 90% and growth rate decreased	Kempinger & Carline 1978
Minimum size limit	none specified	walleye	simulation modeling: lower or no minimum size limits are more likely to decrease total number of fish caught, population biomass, and reproductive potential of the population	Schneider 1978
Creel limits	none specified	smallmouth bass	-creel limits are usually considered unnecessary because few fishermen catch their limit -pressure from some individuals who consider the limit a "goal" may increase	Coble 1975
Minimum size limit (406 mm) and creel	Franklin Delano Roosevelt Reservoir	walleye	-regulations suggested in response to a decline in average age and size of fish -regulations initiated on 1 January, 1985. -initial observations: 50% decline in angler effort, 60% of the fish caught are undersized	Beckman et al. 1985 and Hisata, pers. comm.

Unrestricted creel limits may to increase fishing pressure because anglers would not be restricted by the limit. Removing creel restrictions may initially encourage people to fish more often, because they perceive greater catches. Increasing creel limits and lifting of size restrictions on walleye in John Day Reservoir would not likely increase harvest significantly. A small adult population and an apparent low recruitment of juvenile walleye (Nigro et al. 1985) limits angling interest because catch per unit effort is low. Effects of liberalized regulations on walleye in other Columbia River reservoirs may differ from John Day Reservoir, however. The small average size of walleye in Lake Roosevelt Reservoir was probably caused by over fishing, and restrictions were suggested to prevent a collapse of the fishery (Beckman et al. 1985).

Estimated abundance of smallmouth bass in John Day Reservoir was low relative to walleye and northern squawfish (Nigro et al. 1985). Regulations are liberal because angling effort is light and smallmouth bass are considered underutilized (Steven Williams, Oregon Department of Fish and Wildlife, personal communication). Increasing creel limits with unrestricted size limits would not reduce smallmouth bass populations in John Day Reservoir unless angler effort increased greatly.

There are currently no catch, size or possession limits on angling for channel catfish in John Day Reservoir. Channel catfish may not be common in the reservoir, and few anglers fish for them; most are caught incidentally. Increased channel catfish harvest is unlikely given existing fishing regulations.

The population of northern squawfish was estimated to be the most abundant of the predators under investigation in John Day Reservoir (Nigro et al. 1985). Northern squawfish are not classified as a game fish although, a related species, the Sacramento squawfish, once formed a substantial sport fishery in Clear Lake, California (Taft and Murphy 1950). Northern squawfish concentrate near Columbia River dams during periods of salmonid outmigrations and are vulnerable to fishing (Uremovich et al. 1980). Tournaments similar to the annual series of "fishouts" to remove Sacramento squawfish at Red Bluff Diversion Dam, California (Vondacek and Moyle 1983) may be an effective means to exploit northern squawfish in John Day Reservoir. A bounty on northern squawfish could also be implemented to provide continuous predator control. Over \$300,000 was spent in western Alaska from 1920 to 1941 for bounties on Dolly Varden because they were believed to be serious predators on juvenile sockeye salmon (Morton 1982). Morton (1982) subsequently found that Dolly Varden are no more serious a predator than any other species of trout or char. Such a program should be adequately monitored because abuses have been observed in previous programs. Hubbs (1941) documented that during one Dolly Varden bounty program in Alaska, substantial numbers of rainbow trout and juvenile coho salmon were harvested for bounty.

Presently, three of the four target predators are classified as game fish, and cannot be harvested commercially. If these fish were reclassified, there would be a potential for a commercial fishery. The smallmouth bass population is considered small (Nigro et al. 1985) and would probably not support such a fishery, but walleye and channel catfish are fished commercially in other areas of the country (Tarzwell 1944; Carroll et al. 1961; Elsey and Thomson 1977; Hale et al. 1981) so these species have potential for supporting a commercial fishery in the Columbia River. Northern squawfish could be harvested for the fish meal, protein concentrate, or pet food markets, as it has been considered less palatable than the game species.

A combination of more intensive recreational and commercial harvest might produce the most reduction in population size. A commercial fishery on Lac Des Mille Lacs showed that angling was selective for 4-6 year old walleye, while the commercial fishery mostly harvested fish 5 years and older, (Elsey and Thomson 1977). A large percentage of fish older than 6 years would probably not have been harvested without the commercial fishery and these fish represent a large proportion of the reproductive potential of the population. If recreational anglers generally take smaller channel catfish, or only a small portion of the populations, a commercial fishery would have a much greater impact on the population than the recreational fishery. A modified recreational-commercial harvest might be developed so that sportsman would be allowed to sell their catches, thus creating an incentive for a more intense "recreational" fishery. Special licensing would be required to fund an ongoing monitoring program. There has been considerable commercial harvest of non-game species in the Columbia River for human consumption and other protein supplementation markets (Pruter 1966). Carp, steelhead, salmon, American shad, eulachon, white sturgeon and the Pacific lamprey are or have been harvested with success. Continuation of the fishery was dependent upon market conditions and consumer demand. It has been demonstrated that declining catches and fluctuating market prices may discourage commercial fishermen after an initial "boom" period during the opening of a fishery to commercial harvest (Carroll et al. 1961; Pruter 1966; Elsey and Thomson 1977). A commercial fishery designed to reduce predator populations could be profitable.

Change of release sites Prey protection measures which we judged as having high potential included changing the location and pattern of juvenile salmonid releases. A study on Lake Wenatchee, Washington suggested that predation on sockeye salmon fingerlings by Dolly Varden trout and northern squawfish was greater during hatchery releases than before or after such releases (Thompson and Tufts 1967). Size ranges and presence of fin clipped salmon in predator stomachs confirmed that most were of hatchery origin. Evidently predator congregated at hatchery release sites and preyed heavily on the large concentrations of disoriented prey.

Hatchery release sites should be located and designed to reduce prey concentration and predator congregation although this may cause problems with imprinting. Releases should be avoided when large populations of predators are residing nearby unless predation can be thwarted by deterring or removing predators. Sites where transported fish are released should also be located to maximize survival of juvenile salmonids. Predators, especially northern squawfish, are known to congregate in slack waters near at least two dams on the Columbia River (Gray et al. 1983; Nigro et al. 1985). Similar problems have been observed at the Red Bluff Diversion Dam (RBDD) in California (Vogel and Smith 1984). Salmonids that are released in these areas may be safe as long as they stay within turbulent zones, but may be preyed upon more heavily when they seek out slower water where predators are more prevalent.

Changing smolt bypass locations may also be an effective prey protection measure. Smolt bypass structures are designed to guide fish away from the hydroelectric powerhouse intake through an alternate pathway to reduce turbine-related injury and mortality (Long and Krcma 1969). Fish in the upper portion of the water column are diverted into a collection area where they may be sorted, counted, marked, and released below the dam via the bypass structure. This structure is often a modified sluiceway that releases fish relatively close to the dam (Krcma et al. 1982). The terminal end of the bypass extends into the river a short distance and water pressure expels juvenile salmonids across the upper part of the water column.

When exiting a bypass prey fish are often disoriented and may not be able to effectively avoid predation. Observations of Sacramento squawfish behavior at RBDD bypass outlet by SCUBA divers suggested that release of juvenile salmonids higher in the water column resulted in increased visibility of prey and higher rates of predation (Vogel and Smith 1984). The number and success rates of attacks by Sacramento squawfish were fewer after juvenile salmonids had found cover nearer to the substrate and had begun to school.

There appears to be potential for increasing the survival of juvenile salmonids by changing the design or location of the bypass outlet. A one-time alteration of existing bypass outlets would probably require no more maintenance than the existing outlets, and environmental impacts would be negligible. Locating the terminal end of the release structure nearer to the river bed would reduce the silhouetting effect that has been suggested to increase predation (Keenleyside 1979). Any alteration of existing bypass facilities should consider design strategies to help control predation, including:

- 1) a smooth flow pattern without eddies, flow shears or abrupt changes in velocity.
- 2) positive, unidirectional downstream flow under all flow conditions.

- 3) a multiple outlet bypass system.
- 4) a bottom release bypass outlet.
- 5) artificial turbidity.
- 6) an environment that is not structurally complex since it can result in increased predation by providing locations for waiting predators (Cooper and Crowder 1979 and Delta Fish Facilities Technical Coordinating Committee 1980).

Diel release patterns Researchers have shown the timing of salmonid alevin activity, emergence, and migration is set early in development (Dill 1970; Dill and Northcote 1970; Carey and Noakes 1981) to take advantage of reduced light levels and decrease the probability of detection and capture by predators (Ali 1959; Brett and Groot 1963; Ginetz and Larken 1976). Light sensitivity is so acute among some salmonid species that moonlight can reduce nocturnal migrations (Pritchard 1944; Kobayashi 1964). Predation on coho salmon fry by sculpins has been shown to increase during moonlit nights (Patten 1971). Changes in light intensity, as well as other conditions such as turbidity, current and depth which are presumed to affect hunting efficiency of predators, have been shown to affect the magnitude of migration of juvenile salmonids (Bakshtanskiy et al. 1980). Crepuscular periods may be particularly hazardous times for prey. Visually-oriented predators often hunt during these times (Keenleyside 1979) when prey may be less successful at detecting and avoiding predators. The lights illuminating dams may create an extended artificial crepuscular period and expose juvenile salmonids to increased risk of predation over a longer period of time. At RBDD, evidence from Vogel and Smith (1984) suggests that predation on juvenile salmonids by Sacramento squawfish during day releases was greater than at night with the dam lights turned off.

Release procedures at dams may also produce unnecessary losses of juvenile salmonids. Although salmonids migrate over a 24-hour period throughout the reservoir, they enter bypass facilities mainly at night, peaking between 2200 and 0200 hours (Sims et al. 1981). However, because fish may linger in bypasses for a few to twenty-four hours (Brad Eby, U.S. Army Corps of Engineers, personal communication; Umatilla, OR) they may not exit the bypass at night, which may increase the probability of being eaten by predators.

The releases of hatchery fish and those that are transported may not always be at times that are beneficial to survival. Currently all barged fish are released about midnight. Fish are generally released from trucks at night, although this depends largely upon scheduling conflicts and competing priorities (Donn Park, National Marine Fisheries Service, personal communication). Fish may be released from hatcheries at anytime of the day.

There is potential to increase survival of juvenile salmonids by changing timing of release and altering lighting conditions at dams. Night releases, especially with the lights off or reduced near dams may increase survival of juvenile salmonids.

Number of fish released The migration of juvenile salmonids characteristically is synchronized with distinct peaks in abundance (Basham et al. 1983; Delarm et al. 1984; Koski et al. 1985). Predator population size stays essentially fixed during prey population peaks. Prey behave so as to "swamp" predators over a short period of time and many more prey are encountered than predators could possibly eat. Prey in excess of the limited number eaten by predators will survive. This swamping effect has been shown to reduce the percentage of the population eaten (Table 4). Results of these studies suggest that swamping was at least part of the juvenile salmonid survival strategy. Releasing juvenile salmonids in large numbers should be given high priority for hatchery, barge, and truck release sites because this would reduce predation by creating a swamping effect. At bypass facilities, holding fish for a longer time (instead trickling a few fish out a bypass over 24 hours) and releasing them all at once at night may create such a swamping effect on predators.

Table 4 . Studies on the "swamping" effects of high numbers of prey on predation efficiency.

System location	Prey species	Results	References
Little Togiok River, Alaska	sockeye salmon	-high smolt abundance (20,000 smolts/day) overwhelmed overwhelmed Arctic char. reducing risk of predation	Ruggerone & Rogers 1984
Hooknose Creek, British Columbia	pink and chum salmon	-predators remove relatively fixed number of prey with fluctuating fry abundance affecting the percentage of fry being eaten	Hunter 1959
McClinton Creek, British Columbia	pink salmon	-because predator levels are fairly fixed, prey mortality becomes compensatory at low population levels	Neave 1953

CONCLUSIONS

The results of our initial evaluations indicate that there are several measures that warrant further evaluation, experimentation and development. Predator control measures that appeared to have the highest potential for success were development of a commercial, bounty or recreational fisheries for northern squawfish. Questions on harvest technology, and utilization of harvested fish (i.e. market potential, supply, transportation, holding, storage etc.) and regulation and management of commercial and bounty fisheries need to be addressed. Recreational fisheries for northern squawfish might best be initiated by conducting a "northern squawfish derby".

Prey protection measures that have the highest potential for success were altering dam lighting, release sites, release times, and release numbers/densities. Although these measures may only affect predator losses of juvenile salmonids in the vicinity of the dams, they are measures we can currently control (through project operations and the transportation program) and may be cost effective and easy and quick to evaluate.

The key to implementing any predation control measure will be to develop an effective evaluation technique to determine its success.

LITERATURE CITED

- Allen, K.R. 1955. Factors affecting the efficiency of restrictive regulations in fisheries management. New Zealand Journal of Science and Technology, Section B. 36(4):305-334.
- Ali, M.A. 1959. The ocular structure, retinomotor and photo-behavioral responses of juvenile Pacific salmon. Canadian Journal of Zoology 37:965-996.
- Bakshanskiy, E.L., V.D. Nesterov, and M.N. Neklyudev. 1980. The behavior of young Atlantic salmon, Salmo salar, during downstream migration. Journal of Ichthyology 20(4):93-100.
- Basham, L.R., M.R. DeLarm, S.W. Pettit, J.B. Athearn, and J.V. Barker. 1983. Fish transportation oversight team annual report - FY 1982, Transportation operations on the Snake and Columbia Rivers. United States Department of Commerce, National Oceanic and Atmospheric Administration and National Marine Fisheries Service. National Oceanic and Atmospheric Administration Technical Memorandum NMFS F/NWR-5.88 pp.
- Beamesderfer, R.C., and B.E. Rieman. 1988. Predation by northern squawfish, walleye, smallmouth bass, and channel catfish in a mainstem Columbia River reservoir: III. Estimated abundance and distribution of predators. Transactions of the American Fisheries Society (In Review).
- Beckman, L.G., J.F. Novotny, W.R. Persons, and T.T. Terrell. 1985. Assessment of the fisheries and limnology in Lake F.D. Roosevelt, 1980-1983. Final Report to U.S. Bureau of Reclamation. 168 pp.
- Brett, J.R., and C. Groot. 1963. Some aspects of olfactory and visual responses in Pacific salmon. Journal of the Fisheries Research Board of Canada 20:287-303.
- Carey, W.E., and D.L.G. Noakes. 1981. Development of photo-behavioral responses in young rainbow trout (Salmo gairdneri) Richardson. Journal of Fish Biology 19:285-296.
- Carroll, B-B., G.F. Hall, and R.D. Bishop. 1961. Experimental and contract rough fish removal, Norris Reservoir, Tennessee, 1958-1960. Presented at the annual meeting of the American Fisheries Society, Memphis, Tennessee, Sept. 15, 1961.
- Coble, D.W. 1975. Smallmouth bass. Pages 21-33 in R.H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington D.C. 534 pp.

- Cooper, W.E., and L.B. Crowder. 1979. Predation principles in large rivers: a review. Page 257-268 in H. Clepper, editor. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington D.C.
- Delarm, M.R., L.R. Basham, S.W. Pettit, J.B. Athearn, and J.V. Barker. 1984. Fish transportation oversight team annual report - FY 1983, Transportation operations on the Snake and Columbia rivers. United States Department of Commerce, National Oceanic and Atmospheric Administration and National Marine Fisheries Service. Technical Memorandum National Marine Fisheries Service F/NWR-5-7. 88 pp.
- Delta Fish Facilities Technical Coordinating Committee. 1980. Predation management for the peripheral canal facilities: Working justification paper No. 5. 12 pp.
- Dill, P.A. 1970. On the development of diel activity rhythms in Atlantic salmon and rainbow trout. Ph.D. thesis, University of Western Ontario, London, Ontario.
- Dill, L.M., and T.G. Northcote. 1970. Effects of gravel size, egg depth and egg density on intragravel movement and emergence of coho salmon (Oncorhynchus kitsutch) alevins. Journal of Fisheries Research Board of Canada 27(7):1191-1199.
- Else, C.A., and R.T. Thomson. 1977. Exploitation of walleye (Stizostedion vitreum vitreum) in Lac des Mille Lacs, northern Ontario, by commercial and sport fisheries, 1958-75. Journal of the Fisheries Research Board of Canada 34: 1769-1773.
- Foerster, R.E. and W.E. Ricker. 1941. The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus Lake. Journal of the Fisheries Research Board of Canada 5(4):315-336.
- Ginetz, R.M., and P.A. Larkin. 1976. Factors affecting rainbow trout (Salmo gairdneri) predation on migrant fry of sockeye salmon (Oncorhynchus nerka). Journal of Fisheries Research Board of Canada 33(1):19-24.
- Gray, G.A., and eleven co-authors. 1986. Feeding activity, rate of consumption, daily ration and prey selection of major predators in the John Day Pool. Annual Report (1984) to the Bonneville Power Administration. National Fishery Research Center, Cook, Washington. 163 pp.
- Gray, G.A., G.M. Sonnevill, H.C. Hansel, C.W. Huntington, and D.E. Palmer. 1983. Feeding activity, rate of consumption, daily ration and prey selection of major predators in John Day Reservoir. Annual report to the Bonneville Power Administration. National Fishery Research Center, Cook, Washington. 81 pp.

- Grice, F. 1958. Effect of removal of panfish and trashfish by fyke nets upon fish population of some Massachusetts ponds. Transactions of American Fisheries Society 87:108-115.
- Hale, M.M.M. J.E. Crumpton, and W.F. Godwin. 1981. Game fish by-catch in a commercially-fished hoop nets in the St. Johns River, Florida. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 35:408-415.
- Hanson, D.A., B.J. Belonger, and D.L. Schoenike. 1983. Evaluation of a mechanical population reduction of black crappie and black bullheads in a small Wisconsin lake. North American Journal of Fisheries Management 3(1):41-47.
- Hubbs, C.L. 1941. Predator control in relation to fish management in Alaska. Pages 153-161 in Transactions of the Fifth Annual North American Wildlife Conferences, American Wildlife Institute, Washington D.C.
- Hunter, J.G. 1959. Survival and production of pink and chum salmon in a coastal stream. Journal of the Fisheries Research Board of Canada 16(6):835-886.
- Jeppson, P.W., and W.S. Platts. 1959. Ecology and control of the Columbia squawfish in northern Idaho lakes. Transactions of the American Fisheries Society 88(3):197-202.
- Keenleyside, M.H.A. 1979. Diversity and adaptation in fish behavior. Springer-Verlag. Berlin, Heidelberg, New York. 208 pp.
- Keller, M., and J.V. Manz. 1963. Walleye spawning study in western Lake Erie. Ohio Department of Natural Resources, Federal Fish and Wildlife Restoration Project F-35-R-1, Job Progress Report, Job 1. 29 pp.
- Kempinger, J.J., and R.F. Carline. 1978. Dynamics of the northern pike population and changes that occurred with a minimum size limit in Escanaba Lake, Wisconsin. American Fisheries Society, Special Publication 11:382-389.
- Kobayashi, T. 1964. An ecological study of the salmon fry, Oncorhynchus keta (Walbaum). VII. Note on the behavior of the fry during their seaward migration. Hokkaido Sake, Masu, Fukajo Kenkyu Hokoku. 18:1-6 (In Japanese, English Abstract). (Not seen: cited in Fresh et al. 1980).

- Koski, C.H., S.W. Pettit, J.B. Athearn, and A.L. Heindl. 1985. Fish transportation oversight team annual report - FY 1984, Transportation operations on the Snake and Columbia rivers. United States Department of Commerce, National Oceanic and Atmospheric Administration and National Marine Fisheries Service F/NWR-S-11. 80 pp.
- Krcma, R.F., H.H. Gessel, and F.J. Ossiander. 1983. Research at McNary Dam to develop and implement a fingerling protection system for John Day Dam. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest and Alaska Fisheries Center Seattle, Washington. 24 pp.
- Lawler, G.H. 1965. Whitefish improvement-pike control. Fisheries Research Board of Canada, Biological Station and Technological Unit, Circular No. 7:9-15.
- Long, C.W., and R.F. Krcma. 1969. Research on a system for bypassing juvenile salmon and trout around low-head dams. Commercial Fisheries Review 31:27-29.
- McCrimmon, H.R. 1968. Carp in Canada. Bulletin Fisheries Research Board of Canada 165. 94 pp.
- Meacham, C.P., and J.H. Clark. 1979. Management to increase anadromous salmon production. Pages 317-381 in R.H. Stroud and H. Clepper, editors. Predator-prey systems. Sport Fishery Institute, Washington, D.C. 504 pp.
- Ming, A., and W.E. McDannold. 1975. Effects of length limit on overharvested largemouth bass population. Pages 416-424 in R.H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington D.C. 534 pp.
- Morton, W.M. 1982. Comparative catches and food habits of Dolly Varden and Arctic charrs, Salvelinus malma and S. alpinus, at Karluk, Alaska, in 1939-1941.
- Neave, F. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. Journal of the Fisheries Research Board of Canada 9:45D-491.
- Nigro, A.A. R.C. Beamsderfer, J.C. Elliott, M.P. Faler, L.M. Miller, and B.L. Uremovich. 1985. Abundance and distribution of walleye, northern squawfish and smallmouth bass in John Day Reservoir, 1984. Annual report to the Bonneville Power Administration, Oregon Department of Fish and Wildlife, Clackamas, Oregon. 113 pp.

- NPPC (Northwest Power Planning Council). 1987. Columbia River Basin Fish and Wildlife Program. Adopted November 15, 1982, amended October 10, 1984, and February 11, 1987. Northwest Power Planning Council, Portland, OR.
- Palmer, D.E. and thirteen co-authors. 1986. Feeding activity, rate of consumption, daily ration and prey selection of major predators in John Day Reservoir, 1985.
- Patten, B.G. 1971. Increased predation by the torrent sculpin, Cottus rhotheus, on coho salmon fry, Oncorhynchus kisutch, during moonlight nights. Journal of the Fisheries Research Board of Canada 28 : 1352-1 354.
- Poe, T.P., H.C. Hansel, S. Vigg, L.A. Prendergast, and D.E. Palmer. 1988. Predation by northern squawfish, walleye, smallmouth bass, and channel catfish in a mainstem Columbia River reservoir: I. Feeding ecology during the salmonid smolt out-migration. Transactions of the American Fisheries Society (In Review).
- Priegal, G.R. 1971. Evaluation of intensive drum removal in Lake Winnebago, WI. 1955-1966. Wisconsin Department of Natural Resources, Technical Bulletin 47. 28 pp.
- Pritchard, A.L. 1944. Physical characteristics and behavior of pink salmon fry at McClinton Creek, B.C. Journal of the Fisheries Research Board of Canada 6:217-227.
- Pruter, A.T. 1966. Commercial fisheries of the Columbia River and adjacent ocean waters. Fishery Industrial Research 3(3):17-66.
- Rieman, B.E., R.C. Beamesderfer, L.J. Bledsoe, S. Vigg and T.P. Poe. 1988. Predation by northern squawfish, walleye, smallmouth bass, and channel catfish in a mainstem Columbia River reservoir: IV. Total loss and mortality of juvenile salmonids. Transactions of the American Fisheries Society (In Review).
- Rose, E.T., and T. Moen. 1953. The increase in game fish populations in East Okobojii Lake, Iowa, following intensive removal of rough fish. Transactions of the American Fisheries Society 82:104-114.
- Ruggerone, G.T., and D.E. Rogers. 1984. Arctic char predation on sockeye salmon smolts at Little Togiok River, Alaska. University of Washington Fishery Bulletin, Vol. 82, No. 2.
- Schneider, J.C. 1978. Selection of minimum size limits for walleye fishing in Michigan. American Fisheries Society, Special Publication 11: 398-407.

- Serns, S.L. 1978. Effects of a minimum size limit on the walleye population of a northern Wisconsin Lake. American Fisheries Society, Special Publication 11:390-397.
- Sims, C.W., J.G. Williams, D.A. Faurot, R.C. Johnsen, and D.A. Brege. 1981. Migrational characteristics of juvenile salmon and steelhead in the Columbia River basin and related passage research at John Day Dam, Volumes I and II. Rept. U.S. Army Corps of Engineers. National Marine Fisheries Service, Northwest and Alaska Fisheries Center, Seattle, Washington. 61 pp.
- Taft, A.C., and G.I. Murphy. 1950. The life history of the Sacramento squawfish (Ptychocheilus grandis). California Fish and Game 36(2): 147-164.
- Tarzwel, C.M. 1944. The possibilities of a commercial fishery in the TVA impoundments and its value in solving the sport and rough fish problems. Transactions of the American Fisheries Society 73:137-151.
- Thompson, R.B., and D.F. Tufts. 1967. Predation by Dolly Varden and northern squawfish on hatchery-reared sockeye salmon in Lake Wenatchee, Washington. Transactions of the American Fisheries Society 96(4):424-427.
- Uremovich, B.L., S.P. Cramer, C.F. Willis, and C.O. Junge. 1980. Passage of juvenile salmonids through the ice-trash sluiceway and squawfish predation at Bonneville Dam, 1980. Oregon Department of Fish and Wildlife, Clackamas, OR (Report to U.S. Army Corps of Engineers, Portland, OR).
- Vigg, S., T.P. Poe, L.A. Prendergast, and H.C. Hansel. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: II. Consumption rates of northern squawfish, walleye, smallmouth bass, and channel catfish. Transactions of the American Fisheries Society (In Review).
- Vondracek, B., and P.B. Moyle. 1983. Squawfish predation at Red Bluff Diversion Dam. Contract Report for California Department of Water Resources. 34 pp.
- Vogel, D.A., and J.G. Smith. 1984. Fish passage action program for Red Bluff Diversion Dam. U.S. Fish and Wildlife Service Report FRI/FAO-85-04. 72 pp.

Functional Response of Northern Squawfish Predation to
Salmonid Prey Density in McNary Tailrace, Columbia River

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Abstract

The northern squawfish (Ptychocheilus oregonensis) is a major predator on four species of seaward migrating juvenile salmonids (smolts) in the Columbia River System: steelhead (Salmo gairdneri), sockeye salmon (Oncorhynchus nerka), coho salmon (O. kisutch), and chinook salmon (O. tshawytscha). The functional response of northern squawfish consumption rate to smolt density was evaluated during the migrations (April-August) in the tailrace of McNary Dam; 2391 squawfish containing 1721 salmonid prey were sampled in 1983-1986. Consumption rate was estimated from stomach contents, and smolt density from dam passage counts. The relation between the gravimetric proportion of smolts in the diet and smolt density is described by an exponential saturation model which indicated that squawfish rapidly changed to an almost exclusively salmonid diet at relatively low smolt densities, and that salmonids were always preferred regardless of their density. The observed Type III functional response was described statistically by an exponential sigmoid model that predicted the asymptotic consumption rate to be $5.1 \text{ smolts predator}^{-1} \text{ d}^{-1}$. The corresponding percent mortality curve illustrated mortality was high at the lowest prey densities, compensatory at low to moderate prey densities, and depensatory at high prey densities. The functional response model thus predicts that the effects of predation in McNary Dam tailrace could be reduced by increasing prey densities above present-day maximum levels. Therefore the regional goal of doubling the populations of salmon and steelhead in the Columbia River System, is compatible with the management strategy of minimizing mortality caused by predation. Quantification of the functional response below a mainstem Columbia River dam is prerequisite to understanding predator-prey dynamics, and developing of more complex reservoir-wide or system-wide predation models.

Introduction

Dam-related and in-reservoir mortality of seaward migrating juvenile salmonids (smolts) in the mainstem Columbia River has been estimated to be 10-45% at each project (Raymond 1979; McKenzie et al. 1984; Fish Passage Center (FPC) 1987). The smolt migration at McNary Dam, Columbia River is composed of four species -- steelhead (Salmo gairdneri), sockeye salmon (Oncorhynchus nerka), coho salmon (O. kisutch), and chinook salmon (O. tshawytscha). A population dynamics model has identified mortality rates of smolts in Columbia River reservoirs as being an important component affecting recruitment of salmonid stocks (Northwest Power Planning Council (NPPC) 1986a). Predation is an important component of in-reservoir mortality; others are disease and residualism.

A knowledge of predator-prey relations is fundamental to an understanding of fisheries dynamics. Predation has been recognized as an important biological force in structuring freshwater communities (Hrbacek et al. 1961; Brooks and Dodson 1965; Hall et al. 1970; Zaret and Paine 1973; MacLean and Magnuson 1977; Stewart et al. 1981; Carpenter et al. 1985); and the generalization has emerged that top vertebrate predators are the dominant force (Valiela 1984), e.g., the "keystone" predator concept of Paine (1966). Aside from humans, fishes and birds are the major predators on salmonids in the Columbia River System. Ruggerone (1986) estimated that ring billed gulls (Larus dewarensis) consumed about 2% of the peak spring migration of juvenile salmonids below Wanapum Dam, Columbia River. The northern squawfish (Ptychocheilus oregonensis) is the primary native piscine predator in the Columbia River System (Thompson 1959), and has been implicated in causing substantial depletions of juvenile salmonids in various waters (Ricker 1941; Jeppson and Platts 1967). Estimates of losses of smolts to fish predators in John Day Reservoir, Columbia River indicated that predation accounted for a large proportion of in-reservoir mortality, and that the northern squawfish is the dominant predator (Rieman et al. 1988). Columbia River reservoir fish communities have several species in common with those of Lake Washington which are structured by northern squawfish in a complex way; i.e. predation is significant on both limnetic (salmonids) and benthic-littoral fishes (cottids) but is mediated by prey switching (Eggers et al. 1978).

The "functional response", the effect on individual predator consumption rate caused by changes in prey density (Solomon 1949), is the basis of many predator-prey models (Holling 1959, 1965; Murdoch and Oaten 1975; Hassel 1978; Walters et al. 1978). Predators show two other responses to abundance of their prey: the numerical response (or effect on predator population size), and the developmental response (or effect on predators' morphology and growth) (Solomon 1949; Murdoch 1971, 1973). Holling (1959, 1965, 1966) recognized four classes of functional response curves, each with a characteristic mortality relation: Type I, linear; Type II, decelerating rate; Type III, sigmoid; and Type IV, similar to Type II, except that consumption rate decreases at highest prey densities. Common to all four curves is an upper bound on the rate of consumption per predator at some prey density -- in contrast to the Lotka-Volterra model in which was assumed a linear relation between prey density and the rate of predation

over the entire range of prey densities (Taylor 1984). The asymptote of the functional response may be interpreted as the maximum number of prey that a typical predator can consume per day (C_{max}). This quantity is determined by two factors (1) handling time and (2) satiation level (which is affected by the physical size of the predator's digestive tract, the prey size, and predator physiology).

Peterman and Gatto (1978) remarked on the lack of knowledge of the predation process on salmon -- specifically on the paucity of publications on functional response. Knowledge of predator-prey interactions is especially important to salmonid management, considering (1) that the predation mortality on salmonids in various systems is sometimes as great as 55-85% (Ricker 1941, 1962; Brett and McConnell 1950; Neave 1953; Johnson 1965); (2) predator control programs have seemingly been successful (Foerster and Ricker 1941), and (3) that predation is highly significant in salmonid population dynamics. Hilden (1988) concluded that the type (e.g. II or III) of functional response used in multispecies virtual population analysis has far-reaching consequences, and further suggested that more studies of the predation process in fish communities are prerequisite to gaining deeper insights via such methods. Depensatory mortality processes may cause multiple population equilibria -- as illustrated by the replacement line crossing the stock-recruitment relation in three places (Ricker 1954). Functional response may be an underlying mechanism explaining depensatory mortality and multiple equilibria; e.g. Type III or Type II curve with a non-zero intercept on the X-axis (refugium) may result in multiple equilibria (Peterman 1977). Other causes of multiple equilibria in salmonid populations include the maintenance of productivity by nutrients from the carcasses of spawners, and frequency-dependent competitive interactions (J.M. Emlen, U.S. Fish and Wildlife Service, National Fishery Research Center, Bldg 204, Naval Station, Seattle, WA 98115, pers. comm.)

Recent literature on the functional response of predators to salmonid prey density includes a number of significant studies: predation on fry of chum salmon (*O. keta*) by Pacific staghorn sculpin, *Leptocottus armatus* (Mace 1983); predation on sockeye salmon smolts by Arctic char, *Salvelinus alpinus* (Ruggerone and Rogers 1984); salmonid and cottid predation on chum salmon fry in a small coastal stream (Fresh and Schroder 1987); and feeding by the common merganser (*Mergus merganser*) on coho salmon fry and smolts in a small stream (Wood and Hand 1985). Predation on juvenile salmonids has not previously been described in terms of functional response on a variety of salmonid prey species, nor in a major river system.

My purpose is to describe the functional response of the consumption rate of northern squawfish to variations in density of salmonid preyfish in the tailrace of McNary Dam, Columbia River, during 1983-1986. This functional relation is central to the development of predator-prey models in the John Day Reservoir; furthermore, an understanding of this basic component of the predation process in a representative mainstem reservoir is prerequisite to the formulation of mechanistic models of system-wide population dynamics. Knowledge of the effects of increased numbers of

salmonid smolts on in-reservoir mortality is crucial to the scientific management of the fishery resource in the Columbia River System.

Study Site - Smolt Migrational Characteristics

The Columbia River is the largest river system in the northwestern United States; its basin encompasses 671,000 km². The river is the longest in North America (1,959 km), has the second largest flow in the United States (average of 5,700 m³ · s⁻¹), and is one of the most heavily developed (Trefethen 1972). The Columbia River System was once the greatest producer of chinook salmon and steelhead in the world (Stone 1898; Evans 1977), and still contributes significantly to the salmon and steelhead populations of the Pacific Ocean. The Northwest Power Planning Council, which is the entity responsible for overseeing the provisions of the Pacific Northwest Power Planning and Conservation Act of 1980, adopted an estimate of the annual predevelopment salmonid run of 10 to 16 million adults in the Columbia River System (NPPC 1986); whereas Chapman (1986) estimated 7.5 million adults, not taking harvest by native Americans into account. It is generally agreed that the decline of the fishery, which occurred largely from the early 1930's to the 1970's, was caused by a combination of factors, that included overfishing, construction of dams, and industrial pollution. In recent years the populations of Columbia River salmonids have increased, and a current estimate of the run is about 2.5 million adults (Chapman 1986).

McNary Dam was completed in 1953 at river km 470; downstream from it John Day Reservoir extends 123 km to John Day Dam, which was completed in 1969. The present study was conducted immediately below McNary Dam; in a section of the tailrace referred to here as the boat restricted zone (RZ), is about 0.7 km long, its mean depth is 10 m and the surface area is about 0.46 km² (Fig. 11. The total area of John Day Reservoir is about 210 km².

Annual hatchery production of juvenile anadromous salmonid juveniles upstream from McNary Dam (in the Mid-Columbia and Snake rivers) during 1983-1986 averaged about 35 million fish (FPC 1986). Spring chinook, coho, sockeye salmon, and steelhead generally out-migrate as yearlings; whereas summer and fall chinook salmon out-migrate as sub-yearlings. Most of the smolt migration occurs from April to August; it is composed of about 34.6% yearling and 40.8% sub-yearling chinook salmon, 1.7% coho salmon, 10.3% sockeye salmon, and 12.6% steelhead, as estimated by counts at dams adjusted for percent spill (FPC 1986; Fig. 2).

Environmental characteristics relevant to the smolt migration and predator-prey dynamics vary monthly (Table 1). Temperature varies annually from 0 to 27°C with minima generally occurring in February and maxima in August. Since the implementation of the water budget in 1984 (FPC 1987), maximum weekly mean discharges from McNary Dam of about 840 million m³ · d⁻¹ generally occur in late May to early June, with subsequent declines to minimum weekly mean flows of about 240 million m³ · d⁻¹ occurring during late August to early October.

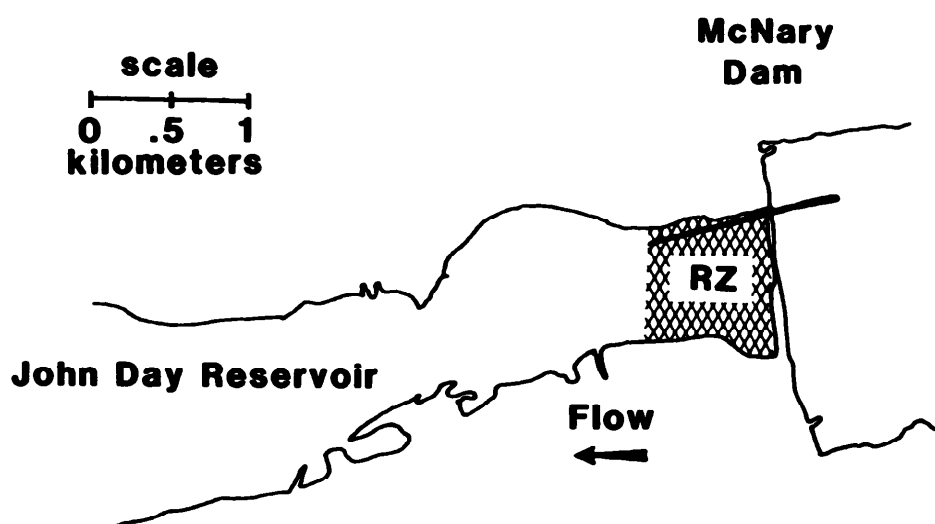
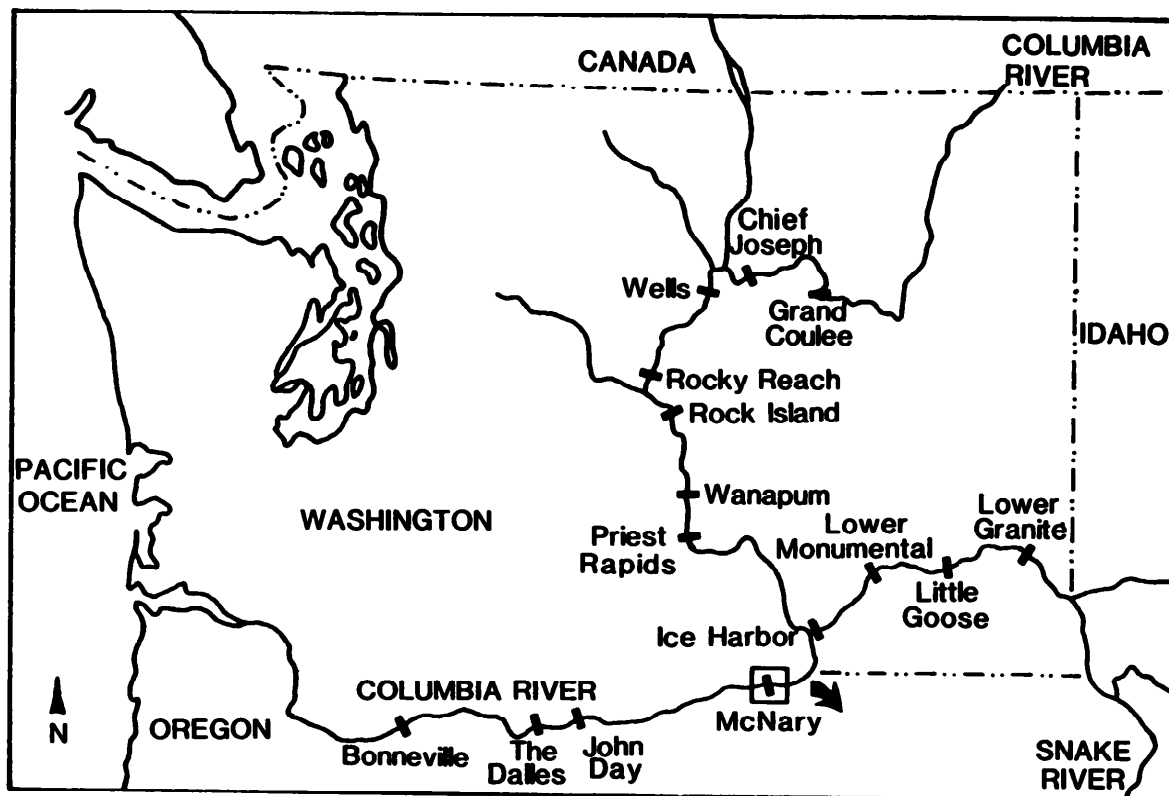


Fig. 1. Location of McNary Dam in the Columbia River System, and the McNary Dam tailrace restricted zone, RZ (shaded).

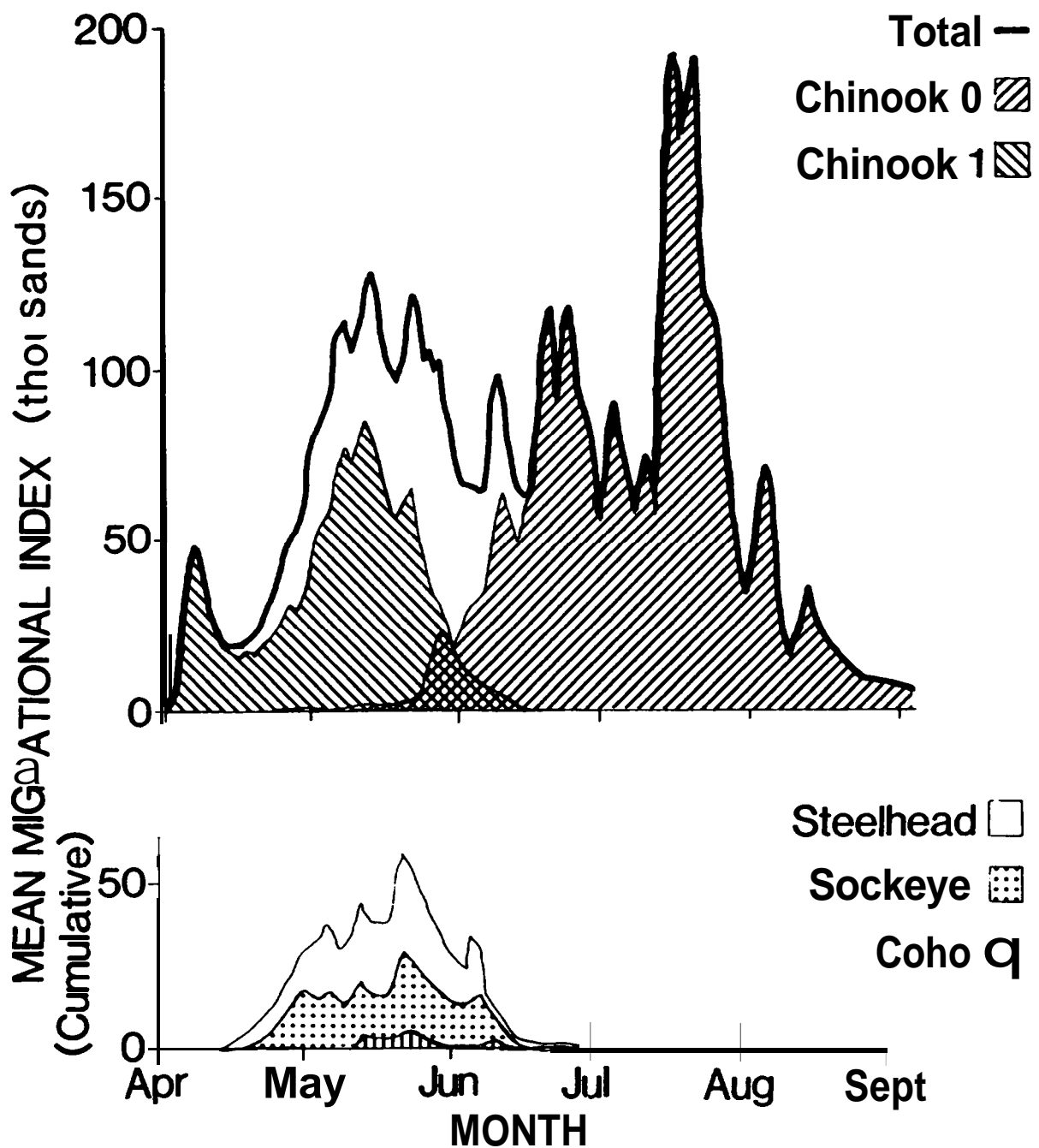


Fig. 2. Timing and relative abundance of the smolt downstream-migration through McNary Dam, Columbia River, 1983-1986.

Table 1. Characterization of environmental and biological conditions at McNary Dam, Columbia River during the out-migration of juvenile salmonids, April-August.

Environmental/ Biological Condition	Month				
	April	May	June	July	August
Day Length ¹ (h)	13.5	14.9	15.7	15.3	14.1
Change	I	I	(P)	D	D
Temperature ² (C)	8.9	11.7	15.5	19.1	21.1
Change	I	I	I	I	(P)
Flow ² (m ³ · 10 ⁶)	587	670	655	406	311
Change	I	(P)	D	D	D
Salmonid Migration Index ² (MI · 10 ⁶)	0.08	0.32	0.25	0.30	0.06
Change	I	(P)	D/I	(P)	D
Salmonid Density ² in tailrace = (MI · 10 ³ · km ⁻²)	1.363	4.776	3.817	7.389	1.929
Squawfish spawning ³		I	(P)	D	
Weight (g) of squawfish ⁴	1146	1140	1153	943	933
Weight (g) of salmonid prey ⁴	42	24	18	12	16
Time to 90% digestion ⁴ (d)	3.0	1.8	0.9	0.7	0.6
Salmonids consumed ⁵ (number · squawfish ⁻¹ · d ⁻¹)	0.2	0.6	0.4	3.4	0.9

1 Daily means, 1983-1986

2 Monthly means, 1983-1986

3 Based on gonadal somatic index 1982, 1986 (S. Vigg, unpubl. data)

4 Monthly means, 1984-1986

5 Consumption estimates, 1983-1986 pooled data (S. Vigg, unpubl. data)

I = Increasing D = Decreasing (P) = Peak

Methods And Materials

Predator Sampling Methods

Northern squawfish were sampled for diet analysis in John Day Pool, below McNary Dam in the RZ each month during the salmonid smolt migration in 1983-1986 (Table 2). Samples were taken on a diel schedule (four, 6-h periods per day for at least three consecutive days) during each month, except in July 1983 and July 1984.

Northern squawfish were sampled primarily with an electroshocker installed in a 5.5-m boat; supplemental methods included a 9-m headrope semi-balloon bottom trawl, and multifilament nylon gill nets measuring 1.8 x 60 m, with meshes of 8.9, 10.2, 12.7, or 15.2 cm (stretched measure). Each predator was weighed, and measured, and the digestive tract was dissected and its contents immediately preserved in 10% formalin. Prey items were later identified to lowest practicable taxon, weighed, and measured; bones were used to help identify fish remains; and body and bone measurements were used to reconstruct the original weights of prey. Detailed descriptions of field and laboratory methods used for fish predator diet analysis in John Day Reservoir were given by Poe et al. (1988).

Consumption Rate Estimates

Consumption rates of the average predator in a sample were calculated with an empirical model that I implemented into computer programs based on a modification of a technique developed by Swenson (1972). The method integrated in situ data on stomach contents with the digestion rate of the predator; it was based on the fact that the level of food observed in the stomach varies as a function of food ingestion and gastric evacuation (Eggers 1977). A regression equation to predict rate of gastric evacuation by northern squawfish from temperature, prey size, and predator size was developed from laboratory experiments by Beyer et al. (1988) and solved mathematically for duration of digestion in hours (t_d):

$$(1) \ t_d = E^{7.16} M^{-0.47} T^{-1.60} W^{-0.27}$$

where E is prey mass evacuated (g), M is meal size (g), T is temperature (C), and W is predator weight (g).

Smolt Density Estimates

Estimates of the number of salmonid juveniles (all species) passing McNary Dam were derived from data collected by the U.S. Army Corps of Engineers and tabulated for 1983 by Sems et al. (1984) and by the FPC for

Table 2. Numbers of northern squawfish collected in McNary Tailrace by month, 1983-1986 (n= 2,391); and (in parentheses) the number of salmonid prey in the stomachs.

Year	Month					Total
	April	May	June	July	August	
1983	2 (0)	79 (70)	65 (25)	0 (-)	94 (14)	240 (109)
1984	58 (11)	64 (53)	95 (24)	0 (-)	117 (43)	334 (131)
1985	69 (77)	76 (90)	91 (49)	74 (120)	88 (11)	398 (347)
1986	118 (38)	205 (177)	365 (152)	518 (713)	213 (54)	1,419 (1,134)
Total	247 (126)	424 (390)	616 (250)	592 (833)	512 (122)	2,391 (1,721)

later years (FPC 1984, 1985, 1986). The "Migrational Index" (MI of the following equation) was used as a daily index of salmonid numbers passing the dam:

$$(2) \text{ MI} = \text{Numbers collected} / (\text{Turbine flow} / \text{Total flow})$$

This index adjusts for the uncounted smolts that pass over the spillway and thus are not subject to sampling by the collection facility at McNary Dam. The MI is generally accepted as the best available estimate of smolt passage, and is the value used by the FPC (FPC 1987).

Migrational Index was converted into a prey density per unit surface area, D (index numbers per km^2) as follows:

$$(3) \text{ } D = \text{MI} \cdot d / f,$$

where d is mean depth (m) of the tailrace restricted zone, and f is mean daily flow ($\text{m}^3 \cdot \text{d}^{-1}$). This measurement assumes prey velocity through the tailrace RZ is proportional to water flow, and implicitly uses residence time of prey items in the RZ in calculation of density. From the perspective of the predator, this adjustment implies either that (1) for a stationary predator, feeding efficiency decreases as the velocity of the prey item increases, or that (2) for a mobile predator, the vulnerability of a preyfish to predation increases proportionally to the length of time the prey remains in the tailrace region.

Analytical Design

Consumption estimates (smolts $\cdot \text{predator}^{-1} \cdot \text{d}^{-1}$) were calculated for each sampling day during which sufficient predators were collected ($n > 15$) to allow a reliable estimate. Smaller samples taken during a period of days when smolt passage was stable were pooled. The number of days required to digest an average juvenile salmonid determined the number of days, previous to the sample day, for which smolt density index estimates were averaged to obtain representative prey density. Turn-over time of prey (Table 3) was estimated from the evacuation rate regression (equation 1) for each month, based on average conditions -- i.e. prey weight, predator weight, and temperature.

At least six factors must be considered for interpretation of functional response data (Table 1, Fig. 2): (1) timing of the out-migration for each species of salmonid, and age group of chinook salmon, (2) migration behavior of smolt groups, (3) size composition of prey, (4) size composition of predators, (5) variables affecting behavior of predators (e.g. spawning), and (6) environmental regime (e.g. day length, temperature, and flow). The most important generalization is that the out-migration can be divided into early and late migrations, separated by a transitional period. The early migration, which occurs in April and May at low temperatures ($< 12.5^\circ \text{C}$) and increasing flows, is composed primarily of chinook salmon yearlings (but includes appreciable numbers of sockeye salmon and steelhead, with a few of

Table 3. Turnover time of salmonid prey in northern squawfish stomachs by month, 1983-1986.

Year	Mean turnover time				
	April	May	June	July	August
1983		1.77	0.64		0.71
1984	2.67	1.82	1.46		0.69
1985	3.13	1.53	0.91	0.51	0.54
1986	3.22	1.98	0.66	0.79	0.63
Mean	3.01	1.78	0.92	0.65	0.64

coho salmon). The late migration, which occurs in July and August at high temperatures (> 17 C) and decreasing flows, consists entirely of smaller sub-yearling chinook salmon. June is a transitional period that includes the end of the run of yearling chinook salmon and the start of the migration of subyearling chinook salmon. Northern squawfish spawning generally peaks during June, and is associated with a reduction in predation rates (Vigg and Prendergast, In Preparation). In addition to the effects of the environment on behavioral interactions between predators and prey under natural conditions, similar factors (e.g. fish size and temperature) are important determinants of the consumption rate estimate because of their effects on the time required for digestion.

Thus, in addition to conducting an overall analysis, I stratified the data into migrational periods (early, transitional, and late) in order to evaluate the effects of smolt density on consumption during homogeneous segments of the migration, and thereby reduce the effects of extraneous factors. Inasmuch as smolt migration index numbers, northern squawfish population size, diet composition, and environmental factors (e.g. water temperature and flow) were relatively constant on an annual basis, and because sample sizes in each year were relatively small, I pooled the data over the four years (1983-1986) for analysis.

Functional Response Models

Least squares multiple linear regression was used to construct empirical models of the relation between squawfish daily consumption rate and biotic and abiotic variables that can logically be postulated to have cause-effect relations with predation.

$$(4) Y = a + B_1X_1 + B_2X_2 + \dots + B_nX_n,$$

where Y = consumption rate, a = intercept, B_n = slopes, and X_n = predictor variables. Transformation of predictor and criterion variables enables the evaluation of various non-linear models (e.g. polynomial and exponential).

Functional response is determined by the bivariate relation between consumption rate (Y) and corresponding smolt density estimate (X). I evaluated several models using least squares linear and non-linear regression methods:

$$(5) \text{ Linear: } Y = a + bX$$

$$(6) \text{ Exponential saturation: } Y = C_{\max} (1 - \exp(-bx))$$

(Gause 1934; Ivlev 1961)

$$(7) \text{ Exponential: } Y = \exp(a + bX)$$

(8) Exponential sigmoid:
$$Y = C_{\max} / (1 + a \exp(-bX))$$

where C_{\max} = maximum consumption, a = intercept, and b = slope.

Although the upper bound or asymptote is a fundamental theoretical basis for functional response models, the saturation level may not be observed for a given data set in nature. Under these conditions, the linear fit would represent a Type I functional response and an exponential model would represent a Type III. When the saturation level is reached in a data set, the exponential saturation model represents Type II and the exponential sigmoid is represents Type III.

Results

Empirical Models of Consumption Rate on Environmental Variables

Multiple linear regression models of the daily consumption rate (smolts $\text{predator}^{-1} \text{ d}^{-1}$) of northern squawfish on abiotic and biotic variables for the entire study period (all data pooled) demonstrated relations with prey density, temperature, and prey weight (Table 4). Stepwise regression, in which statistical criteria were used for selection of variables, indicated that prey density accounts for the largest proportion of the variability in consumption rate -- both for linear and polynomial relations. Water temperature and prey weight also exhibit statistical relations with the number of smolts eaten by squawfish but, unlike prey density, are not truly independent variables since they are important determinants of the calculation of the consumption rate estimates by the evacuation rate regression (equation 1). Although a relatively large proportion of the variability in consumption (72-77%) is statistically explained by these multivariate empirical models, it is tenuous to interpret these results in terms of predation theory.

Functional Response

An exponential sigmoid model (equation 8), Type III functional response provided the best statistical fit of the relation between consumption rate of northern squawfish on smolts and prey density for the entire study period ($R^2 = 0.77$, $n=51$; Fig. 3). This model predicts a daily maximum consumption rate of 5.1 smolts per predator. Functional Response during April and May was best described by an exponential model (equation 6; $R^2 = 0.72$). Smolt densities ($< 3000 \text{ MI } \text{km}^{-2}$) were low during this period, and the asymptotic phase of the response was not apparent. During June there was a poor, if any relation between smolt density and consumption rate by squawfish; however the data could be fitted using a Gause-Ivlev, Type II, model ($R^2 = 0.23$). The July-August data included a wide range of smolt densities, and saturation of consumption rate was apparent at densities $> 3500 \text{ MI } \text{km}^{-2}$. These data were best fitted by an exponential sigmoid model ($R^2 = 0.91$).

Table 4. Empirical multiple linear regression models of northern squawfish daily consumption rate (number l predator⁻¹ d⁻¹) on various predictor variables in McNary tailrace restricted zone, April-August 1983-1986(n= 51).

Model	Independent variables ¹	Coefficient	Significance level		R ²
			Coefficient	F for Regression	
A	Constant	-0.74754	0.0016	<0.0001	0.717
	N	0.00046	<0.0001		
	T	0.04753	0.0037		
B ²	Constant	-1.28206	0.0067	<0.0001	0.748
	N	0.00046	<0.0001		
	(T) ³	0.00011	0.0001		
	ln(W)	0.26863	0.0396		
C ³	Constant	-0.21908	0.1018	<0.0001	0.768
	(N) ²	1.923 E-7	<0.0001		
	(N) ³	-1.489 E-11	<0.0001		
	(T) ²	0.00163	0.0017		
D	Constant	0.45265	0.0179	<0.0001	0.739
	(N)	-0.00063	0.0374		
	(N) ²	4.400 E-7	0.0004		
	(N) ³	-3.354 E-11	0.0005		

1 Variables available for selection included N= prey density, T= temperature, W= prey weight, predator weight, and river flow; and the natural log, square, and cube of each variable.

2 Variables identified using forwards stepwise selection.

3 Variables identified using backwards stepwise selection.

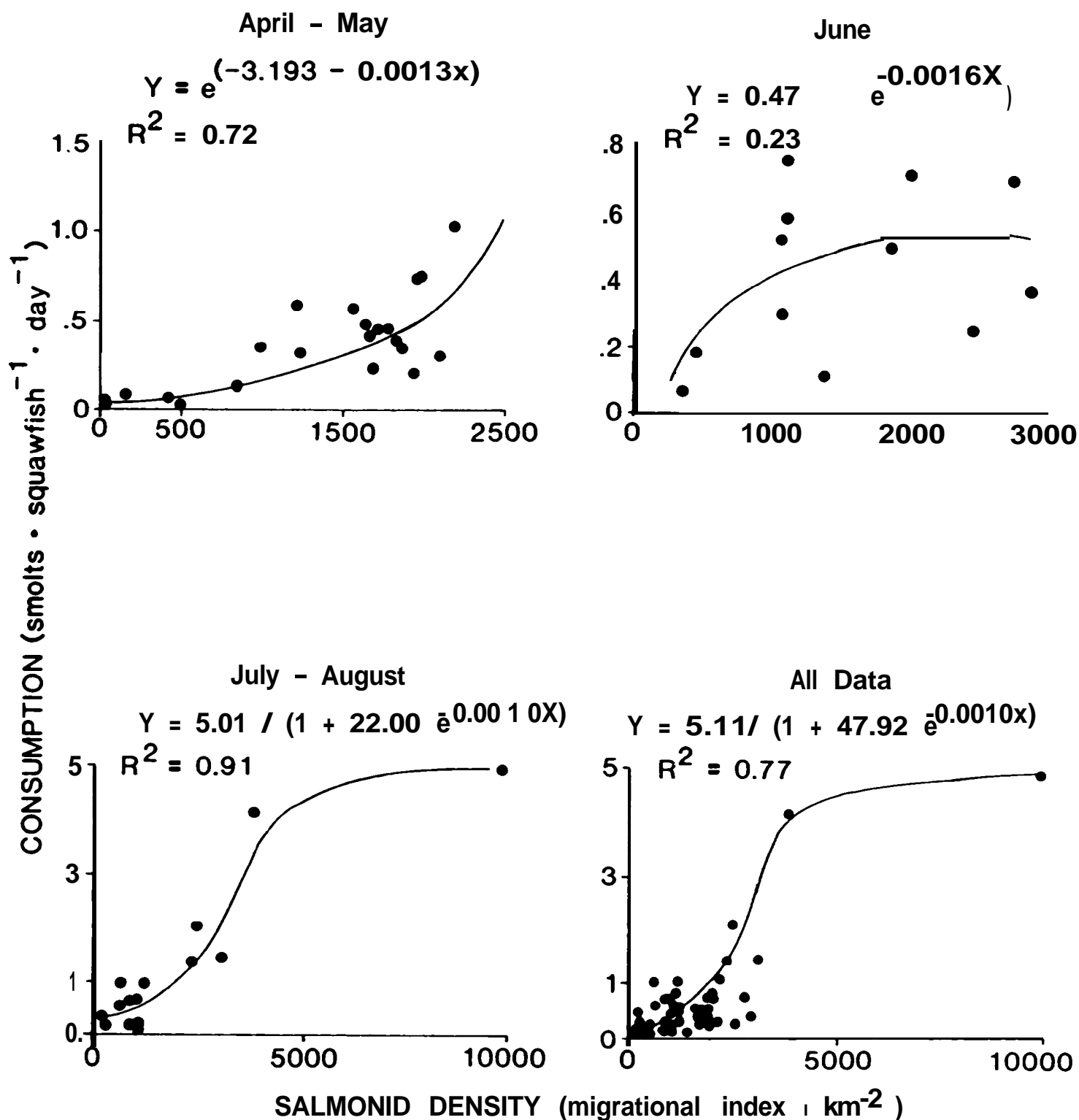


Fig. 3. Functional response models (-) of salmonid consumption by northern squawfish versus salmonid prey density in the tailrace of McNary Dam, Columbia River, stratified by time period and pooled 1983-1986.

Biological rationale related to spawning behavior of squawfish and the migrational characteristics of smolts (further discussed later) suggest that the underlying functional response may be best described by eliminating the June data. A sigmoid exponential functional response model for the April-May and July-August periods combined ($R^2 = 0.87$; Fig. 4, top) has essentially the same asymptote as the overall and July-August relations (about 5.1), since the maximum prey densities and consumption rates occurred only in July. The relation analogous to functional response, but in terms of ration (Fig. 4, bottom) is useful for comparisons over the entire smolt migration since predator and prey sizes vary over the course of the migration and ration standardizes consumption relative to fish weight (prey weight \div predator weight⁻¹). The asymptotic daily ration estimated by the logistic model is about 58 mg of salmonids per gram of squawfish. Percent of the smolts (density index) consumed per predator derived from the functional response model illustrates (1) a high mortality rate followed by a steep decline at very low smolt densities, (2) a compensatory phase (accelerating rate) at low to moderate densities, and (3) a depensatory phase (decelerating rate) at densities greater than about 4500 MI \div km⁻² (Fig. 5).

Prey Density Effects on Diet Composition

An exponential saturation model (equation 5) describes the rapid increase in the proportion of salmonids (by weight) in the diet of northern squawfish compared to non-salmonid preyfish, associated with increases in salmonid prey density during the April-May and July-August periods (Fig. 6). If the non-salmonid prey population is assumed to remain constant, then the x-axis represents the proportion of salmonids in the environment; therefore Fig. 6 would represent a preference curve in the sense of Ivlev's (1961) forage ratio. During June there is no significant relation ($P > 0.05$) between the percent composition of salmonids in the diet and smolt density -- further illustrating the inconsistent predator-prey relations during this period. The model fitted to mean percent salmonids in the diet, stratified by prey density, for the April-May and July-August periods combined, illustrates that the northern squawfish diet approached the asymptotic value of 100% salmonids when smolt density exceeded about 2500 MI \div km⁻² ($R^2 = 0.88$; Fig. 7).

Discussion

Observed Functional Response in Terms of Predation Theory

Multiple linear regression showed that, of the possible predictor variables measured, prey density explained the largest proportion of the variability in northern squawfish consumption rate of smolts in McNary tailrace during 1983-1986. This method alone, however, does not adequately fit the apparent non-linearities of the data nor give insight into the underlying theoretical processes of predation.

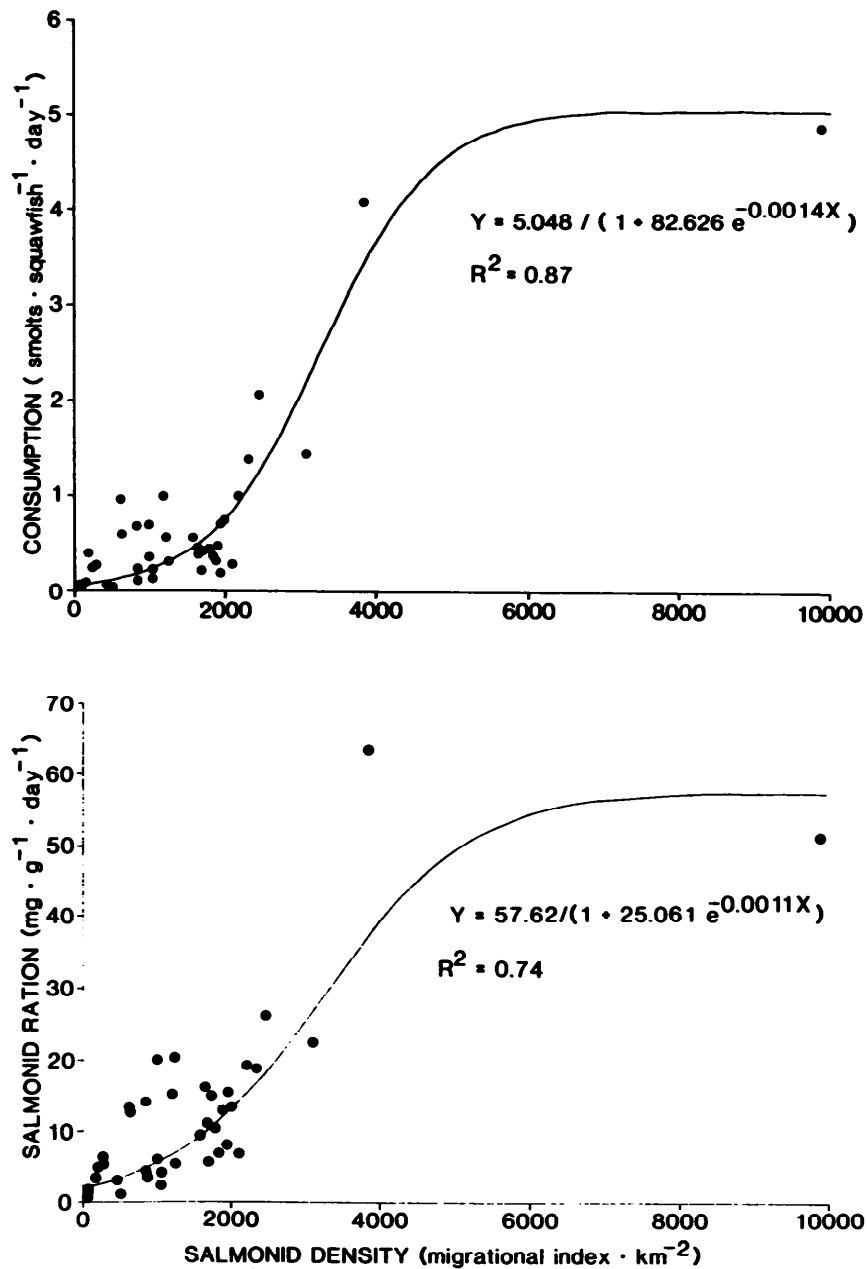


Fig. 4. Exponential sigmoid functional response of daily numerical consumption (top) and ration (bottom) of salmonid smolts by northern squawfish versus salmonid density in the tailrace of McNary Dam, Columbia River during April, May, July and August, 1983-1986.

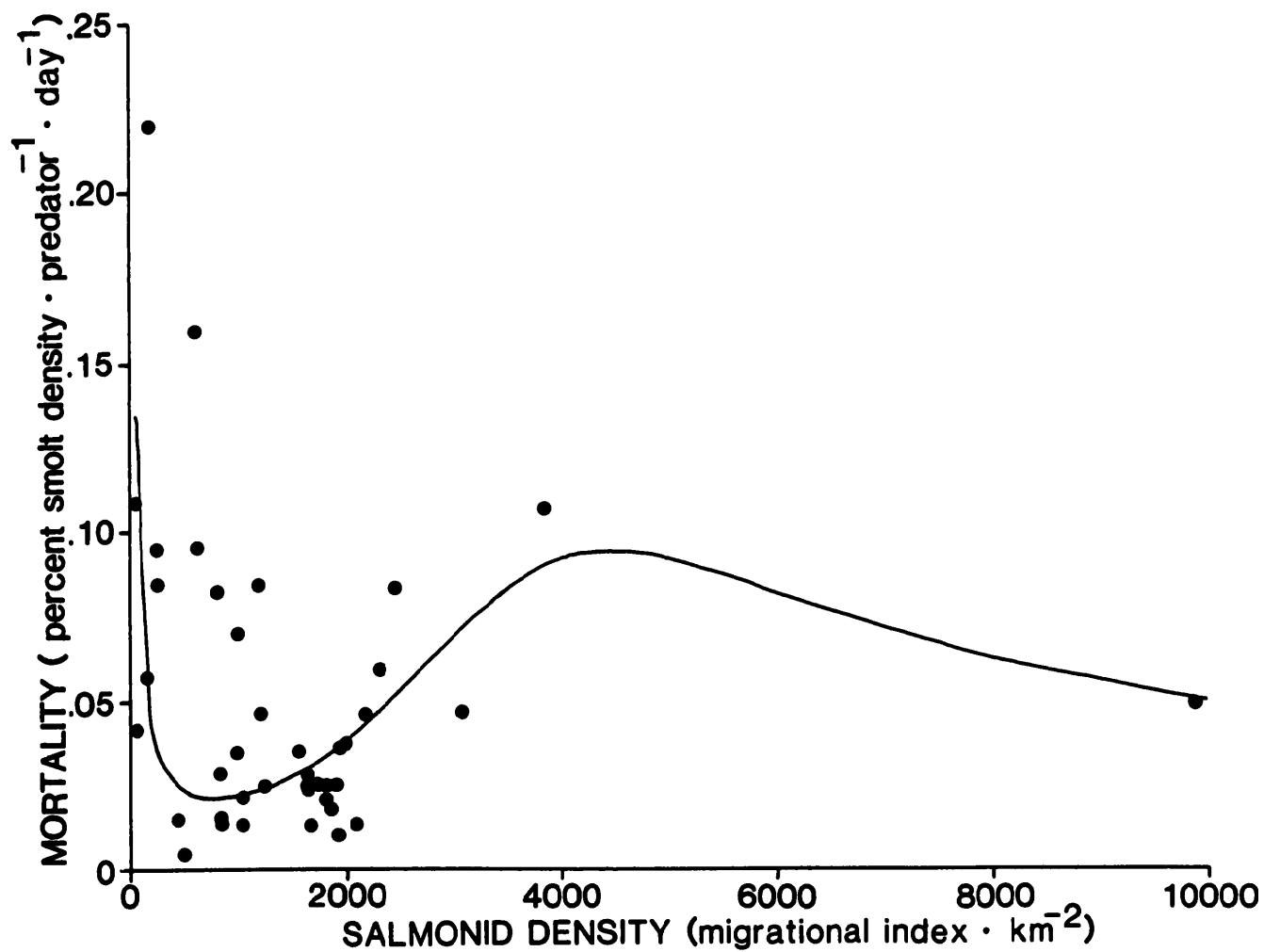


Fig. 5. Consumption mortality rate per predator of smolt population in McNary Dam tailrace, Columbia River 1983-1986 based on the exponential sigmoid functional response model.

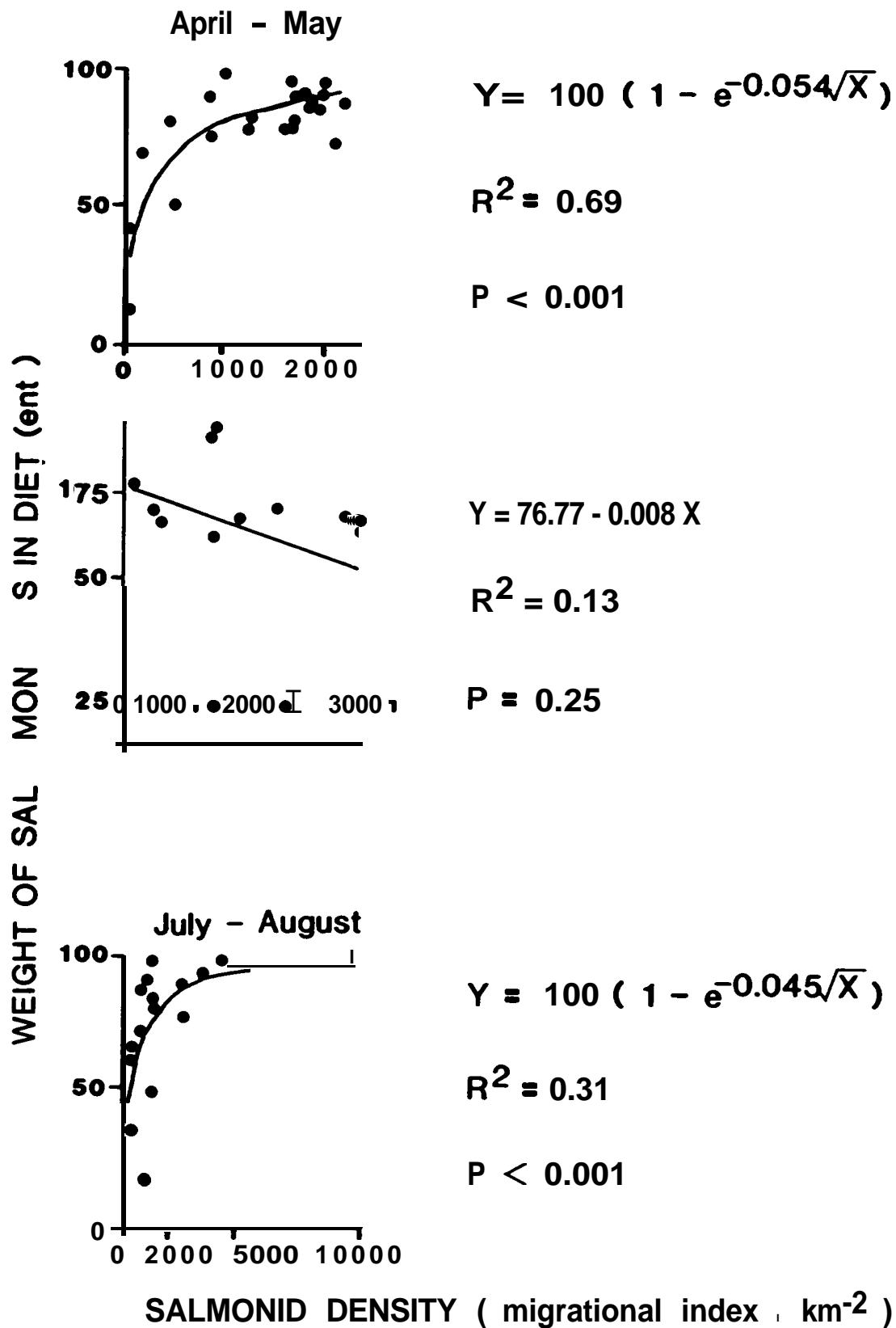


Fig. 6. Percent weight of salmonids in the diet of northern squawfish versus salmonid prey density in the tailrace of McNary Dam, Columbia River, stratified by monthly time period, 1983-1986.

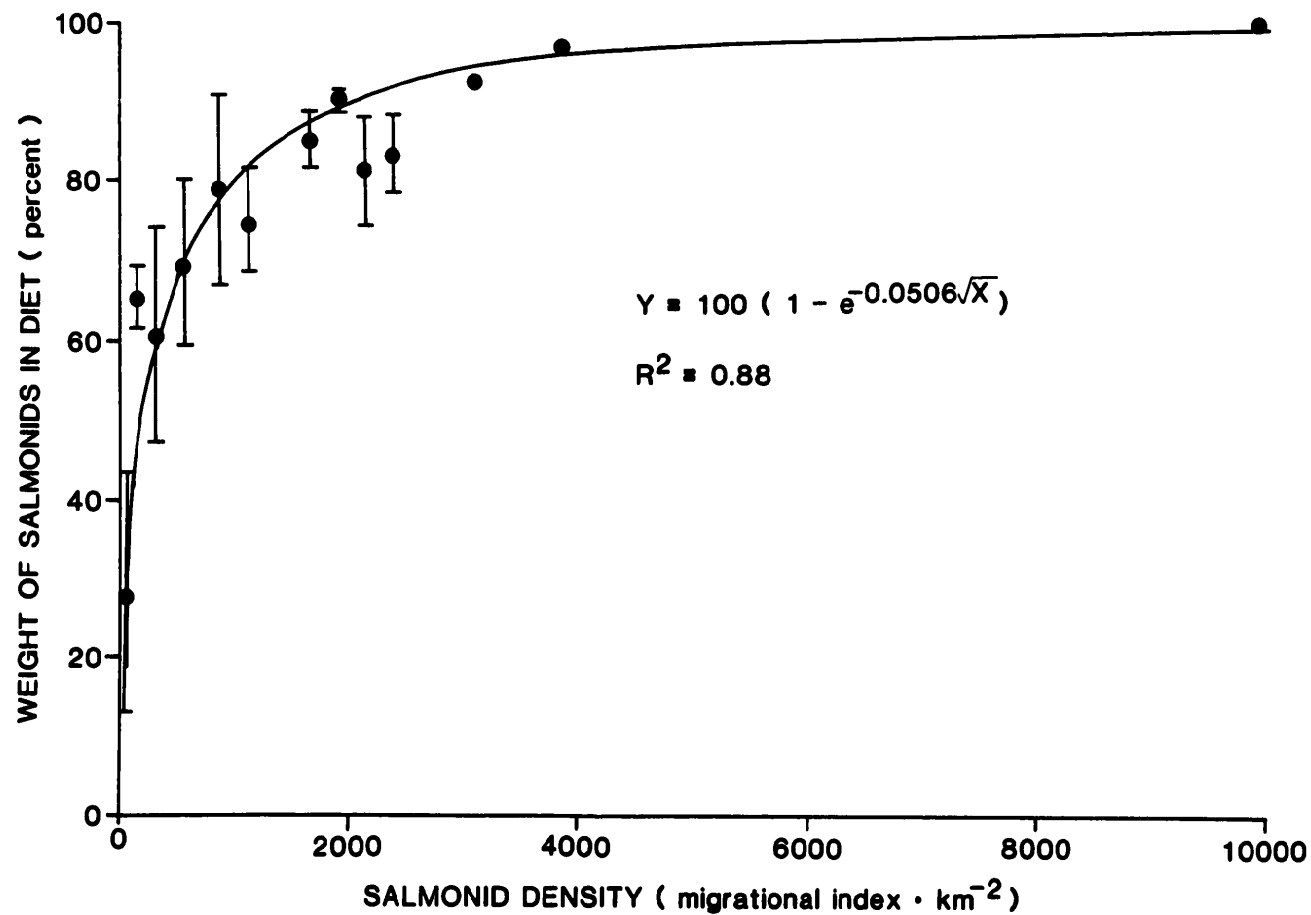


Fig. 7. Exponential saturation model fitted to mean percent weight of salmonids in diet by prey density strata (·); vertical bars indicate standard error of the mean.

A sigmoid curve, Type III functional response, best described the response of northern squawfish predation rate to concurrent smolt densities over the entire period of seaward migration. This observation is consistent with ecological theory, which states that Type III functional response is typical of vertebrate predators (Holling 1959; Tinbergen 1960). Avian and fish predators of juvenile salmonids usually exhibit a Type III functional response when more than one type of prey is available (Murdoch and Oaten 1975; Peterman and Gatto 1978). Phenomena associated with learning often show the classical sigmoid response, and aspects of learning have been postulated as mechanisms underlying the Type III functional response; however, Murdoch (1973) points out the criterion for the Type of functional response is the form of the curve (i.e., result of predation) and not the mechanism (i.e., presence or absence of learning) since there is not a one-to-one relationship between form and mechanism. Peterman (1977) describes various mechanisms which can result in a Type III functional response.

Tinbergen (1960) used the term specific search image to describe how birds learned to search for prey. Holling (1965) analyzed the effect associative learning on the functional response, and demonstrated that predator experience with different food items was sufficient to simulate the sigmoid relation between intensity of predation and prey density -- which is characteristic of searching image formation. Reactive distance of fish predators can be increased by experience with specific prey (Beukema 1968, Ware 1971).

Transition of predation from one prey species to another, may involve learning in various aspects of predator-prey interactions; e.g. prey distribution patterns, size, swimming speed, and escape response versus predator hunting patterns, image recognition, chasing, and handling skills. If the change from one prey species to another involves negative preferential selection (in the sense of Ivlev's (1961) forage ratio) for the species at low abundance to positive selection for the species at high abundance, then it is termed "switching" (Murdoch 1969). The exponential saturation model of proportion of salmonids in the diet of northern squawfish (Fig. 7) shows that the squawfish rapidly changed from non-salmonid to a predominantly smolt diet at relatively low smolt densities (including most of the migrational period); however "switching" did not occur since the form of the curve indicates a strong positive preference for smolts occurred over the entire range of smolt densities (Murdoch and Oaten 1975). The transition of squawfish predation from one salmonid prey species to another however, may involve "switching" on to high density patches. From the strategic, as opposed to the mechanistic perspective, optimal foraging theory might explain a sigmoid functional response in terms of maximizing benefit: cost by having catches mediate predatory effort expended (Taylor 1977, 1984). Ware (1972) postulated that rainbow trout (Salmo gairdneri) must exceed a threshold rate of capture before they will persist in a particular hunting pattern.

Predators have been observed to exhibit different types of functional responses at different times of the year when prey density and composition

changes (Runge 1980; Valiela 1984). The smolt migration through McNary tailrace is composed of three segments: (1) yearling chinook, coho, and sockeye salmon and yearling steelhead during April and May; (2) a decline of these groups concurrent with the beginning of sub-yearling chinook salmon migration in June; and (3) peak abundances of the sub-yearling chinook salmon population in July, followed by a decline in August (Fig. 2). The exponential relation observed during April-May is consistent with a Type III functional response in which smolt densities are not high enough to reach the asymptotic consumption rate. The apparent lag in predator consumption responding to increasing prey densities may be related to the predator population gaining experience in preying on four different species of prey during the early migration. Likewise, a sigmoid functional response was observed during July and August after the prey composition had changed from a mixture of species to sub-yearling chinook salmon, which probably have different behavior and distribution patterns. Decreases in benefit: cost as the smolt abundance subsided in August may help explain the exponential phase of the curve at low densities.

The apparent lack of functional response during June is anomalous, but might be explained by consideration of two factors: (1) a change of predatory efficiency during the period of transition of prey composition, and (2) a change in priorities of energy expenditure by northern squawfish during spawning. The proportion of gonad weight to somatic weight indicated that spawning of northern squawfish in John Day Reservoir peaked during June, both in 1982 and 1986 (Vigg and Prendergast, In Preparation). Northern squawfish spawn in a variety of habitats and depths, but the grounds are characterized by clean rocky substrate near low-velocity currents; aggregations of hundreds of fish showing high activity characterized by chasing behavior is typical (Casey 1962; Patten and Rodman 1969; Olney 1975; Beamesderfer 1983). During June large segments of the squawfish population in the tailrace probably moved from prime feeding areas (e.g. near turbine discharge and smoltbypass facilities) and expended a larger proportion of their energy on reproductive, as opposed to feeding activities. The larger percent of empty stomachs during June (31.3) compared to May (17.7) and July (24.5) for northern squawfish in the McNary tailrace RZ, in 1983-1986 (unpubl. data) provide further evidence of depressed feeding.

Management Implications of Functional Response

The results of this study support the conclusions of Peterman and Gatto (1978), who suggested that predators on juvenile salmon are not generally swamped by any but the very largest prey populations. On only two occasions during this study (July 1985 and 1986) were prey densities high enough to reach an apparent asymptote of the functional response relation. Thus, given current salmonid population abundance, only the highest daily passage rates, and corresponding prey densities, through McNary tailrace would cause the maximum consumption rates of northern squawfish to be exceeded. The maximum consumption of $5.1 \text{ smolts} \cdot \text{squawfish}^{-1} \cdot \text{d}^{-1}$ predicted from the Type III functional response is within the range of tests to experimentally determine maximum consumption rates of northern squawfish

in a laboratory environment (unpubl. data); and is consistent with the maximum consumption rate (i.e., 5.8 salmon / squawfish⁻¹ d⁻¹) reported by Vondracek (1988) for Sacramento squawfish (*P. grandis*) feeding on juvenile chinook salmon below the Red Bluff, California, diversion dam.

Functional responses of piscine predators reported in the literature have been predominantly Type II (e.g. Ware 1972; Swenson 1977; Mace 1983; Ruggerone and Rogers 1984; Fresh and Schroder 1987; Lyons 1987). However, this study represents the first quantification of functional response of a large piscine predator population feeding on several salmonid species in a large river system over a wide range of smolt densities during several years. Theory predicts that a normally distributed population of predators that individually show Type II functional responses with a prey threshold (zero attack rate at non-zero prey densities) will result in an aggregate S-shaped (Type III) curve (C.J. Walters, as cited in Peterman 1977).

The percent mortality curve derived from the functional response relation (Fig. 5) illustrates compensatory mortality at very low and very high prey densities; this phenomenon would theoretically provide equilibria at both extremes (Noy-Meir 1975; Valiela 1984). The resultant refugium at low densities could prevent predation from causing extinction if salmonid abundance were severely depressed (as it was historically in the Columbia River). Compensatory mortality occurs at low to moderate prey densities, which includes most smolt migrations during recent years. The implication is that predation has its maximum effect under present conditions. The compensatory phase at high prey densities indicates that increases over present-day levels of smolt passage would diminish the effect of predation and increase the effectiveness of enhancement programs. Smolt abundances in the upper Columbia River are likely to increase in the next decade due to current increases in adult runs, improvement of natural spawning habitat, continued improvement of smolt passage facilities at dams, and projected increases in hatchery production. The NPPC is committed to doubling the runs of adult salmon and steelhead over those in 1976-1981 (NPPC 1987). Therefore, quantification of the response of predation rate to increases in prey density is important to future management strategies.

The nature of the observed functional response suggests that several management measures are feasible in the Columbia River System to mollify the effects of predation by manipulating prey density. Releases of various upriver hatcheries could be timed to synchronize the passage at dams where major predation losses occur. Manipulation of the temporal pattern of flow (water budget) can be implemented to reduce the residence time of pulses of smolts in tailraces of dams. Facilities could be constructed at dams to hold smolts for a period of hours, and release them in high density pulses during optimal diel periods. Ongoing transportation of smolts with trucks and barges, can be evaluated in terms of shifting smolt densities from the compensatory phase of the functional response to one of the compensatory regions.

Limitations of the Data

Estimates of consumption rate and prey density are difficult and expensive to obtain in large river-reservoir systems. Most of the data available to formulate the functional response model were in the low to moderate range of prey density and consumption; few data were available at maximum levels. Additional research is needed to quantify the variability of the functional response components at the upper end of the relation.

Improvements in smolt passage estimates at McNary Dam, and any other project of interest, will be necessary to refine description of the functional response relation in John Day Reservoir or system-wide. Giorgi and Sims (1987) presented a method to estimate daily passage of juvenile salmonids at McNary Dam, which is based on species and age group-specific calibration curves for collection efficiency at the smolt bypass facility over a range of powerhouse flows. This method provides estimates of the total number of smolts passing the dam, as opposed to the MI which is only an index of abundance. Several deficiencies, however, precluded the use of the Giorgi and Sims (1987) passage estimate method: (1) uncertainties in temporal changes in guidance efficiency of the traveling screens that deflect smolts from the turbine intake into the collection facility, caused by changes in behavior and vertical distribution of the smolts; (2) imprecision of calibration curves, i.e. powerhouse discharge level accounted for less than half of the variability in collection efficiency ($R^2 = 0.41, 0.37$); (3) calibration curves are applicable only over a restricted range of percent powerhouse flows (28-76%), which is often exceeded; and (4) no collection efficiency relation has been developed for coho, sockeye, and (most important) subyearling chinook salmon, which are the most abundant single group of smolts.

If the shape of the functional response in the McNary tailrace is representative of the northern squawfish-smolt predation rate relationship in John Day Reservoir (where large losses of smolts may occur), then it may be applied by using observed consumption in the reservoir as a scaling factor. However, accurate residence time relations are required for each group of smolts. At present, residence time-flow relations have been developed for yearling steelhead and chinook salmon; but the residence time estimates for sub-yearling chinook salmon are quite variable and are not consistently related to flow (Miller and Sims 1984).

Summary and Conclusions

Since smolt density in the Columbia River will likely increase in future years, the Type III functional response model quantified in this study has important ramifications to the management of salmon and steelhead in the system. This model is consistent with general ecological predation theory, and what is expected when a piscine predator feeds on more than one prey species. The asymptote of the model (5.1 smolts/predator $\cdot d^{-1}$) is consistent with available in situ and laboratory information for

squawfish feeding on salmonids. The percent mortality curve, based on the functional response model, illustrates that predation can have a compensatory effect at present salmonid population levels and will have a diminishing proportional impact if prey densities are substantially increased. In addition to increasing the salmonid population size via increased reproduction, the effective prey densities of smolts can be increased using such techniques as pulsing, synchronization of hatchery releases, reduction of structure-related passage mortality, and judicious use or non-use of transportation. Increasing the relative abundance of alternate prey fish would probably not reduce predation by squawfish, because salmonids are strongly preferred over the entire range of salmonid densities and there is no indication that "switching" to non-salmonids would occur.

Further research on squawfish consumption rates at high prey densities, and better estimates of numbers of smolts passing McNary Dam are needed to refine the functional response relation. Accurate and more precise estimates of residence time of smolts, especially sub-yearling chinook salmon in John Day Reservoir will be required to extrapolate the functional response observed in McNary tailrace to the entire reservoir. Development of the functional response in a major reservoir, such as John Day, should facilitate the formulation of a system-wide mechanistic model of predator-prey dynamics in the Columbia River System.

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References

- Beamesderfer, R.C. 1983. Reproductive biology, early life history, and microhabitat of northern squawfish (Ptychocheilus oregonensis) in the St. Joe River, Idaho. M.S. thesis. University of Idaho. Moscow, ID 144 p.
- Beukema, J.J. 1968. Predation by the three spined stickleback (Gasterosteus aculeatus L.): the influence of hunger and experience. Behavior 31: 1-126.
- Beyer, J.M. G. Lucchetti, and G. Gray. 1988. Digestive tract evacuation in northern squawfish (Ptychocheilus oregonensis). Can. J. Fish. Aquat. Sci. 45:548-553.
- Brett, J.R., and J.A. McConnell. 1950. Lakelse Lake sockeye survival. J. Fish. Res. Board Can. 8: 103-110.
- Brooks, J.L., and S.I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150: 28-35.
- Carpenter, S.R., J.F. Kitchell, and J.H. Hodgson. 1985. Cascading trophic interactions and lake productivity - fish predation and herbivory can regulate lake ecosystems. Bioscience 35: 634-639.
- Casey, O.E. 1962. The life history of the northern squawfish in Cascade Reservoir. M.S. thesis. University of Idaho. Moscow, ID.
- Chapman, D.W. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth century. Trans. Am. Fish. Soc. 115: 662-670.
- Eggers, D.M. 1977. Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Can. 34: 290-294.
- Eggers, D.M., N.W. Bartoo, N.A. Rickard, R.E. Nelson, R.C. Wissmar, R.L. Burgner, and A.H. Devol. 1978. The Lake Washington ecosystem: the perspective from the fish community and forage base. J. Fish. Res. Board Can. 35: 1553-1571.

- Evans, D.J. 1977. Keynote address, p. 13-19. In E. Schwiebert (ed.) Columbia River salmon and steelhead. Am. Fish. Soc. Spec. Publ. No. 10. Washington, DC.
- FPC. 1984. Smolt monitoring program, annual report, BPA DOE/BP-354. Fish Passage Center, Portland, OR.
1985. Smolt monitoring program, annual report, 1985. BPA Project Agreement No. DE-A179-83-BP11797. Fish Passage Center, Portland, OR.
1986. Smolt monitoring program, annual report, 1986. BPA Project No. 86-60, Agreement No. DE-A179-86BP61747. Fish Passage Center Portland OR.
- Foerester, R.E., and W.E. Ricker. 1941. The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus Lake J. Fish. Res. Board Can. 5: 315-336.
- Fresh, K.L., and S.L. Schroder. 1987. Influence of the abundance, size, and yolk reserves of juvenile chum salmon (Oncorhynchus keta) on predation by freshwater fishes in a small coastal stream. Can. J. Fish. Aquat. Sci 44: 236-243.
- Gause, G.F. 1934. The struggle for existence. The Williams and Wilkens co., Baltimore.
- Giorgi, A.E. and C.W. Sims. 1987. Estimating the daily passage of juvenile salmonids at McNary Dam on the Columbia River. N. Am. J. Fish. Manage. 7: 215-222.
- Hall, D.J. W.E. Cooper, and E.E. Werner. 1970. An experimental approach to the population dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 15: 839-928.
- Hilden, M. 1988. Significance of the functional response of predators to changes in prey abundance in multi-species virtual population analysis. Can. J. Fish. Aquat. Sci. 45:89-96.

- Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91: 385-398.
1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* No. 45.
1966. The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* 48: 1-85.
- Hrbacek, J., M. Dvorakova, V. Korinek, and L. Prodhazkova. 1961. Demonstration of the effect of fish stock on the species composition of zooplankton and the intensity of metabolism in the whole plankton assemblage. *Verh. Int. Ver. Theoret. Angew. Limnol.* 14: 192-195.
- Hunter, J.G. 1959. Survival and production of pink and chum salmon populations in British Columbia. *J. Fish. Res. Board Can.* 16: 835-886.
- Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, CT.
- Jeppson, P.W., and W.S. Platts. 1959. Ecology and control of the Columbia squawfish in northern Idaho lakes. *Trans. Am. Fish. Soc.* 88: 197-202.
- Johnson, W.E. 1965. On mechanisms of self-regulation of population abundance in Oncorhynchus nerka. *Mitt. Int. Ver. Theor. Angew. Limnol.* 13: 66-87.
- Lyons, J. 1987. Prey choice among piscivorous juvenile walleyes (Stizostedion vitreum) *Can. J. Fish. Aquat. Sci.* 44: 758-764.
- Mace, P.M. 1983. Predator-prey functional responses and predation by staghorn sculpins (Leptocottus armatus) on chum salmon fry (Oncorhynchus keta). Ph.D. thesis, University of British Columbia, Vancouver, B.C. Canada.
- MacLean, J., and J.J. Magnuson. 1977. Species interactions in percid communities. *J. Fish. Res. Board Can.* 34: 1941-1951.

- McKenzie, D., D. Weitkamp, T. Schadt, D. Carlile, and D. Chapman. 1984. 1982 Systems mortality study. Prepared for Chelan, Grant, and Douglas County P.U.D.s by Battelle, Pacific Northwest Laboratories, Richland, WA.
- Miller, D.R., and C.W. Sims. 1984. Effects of flow on the migratory behavior and survival of juvenile fall and summer chinook salmon in the John Day Reservoir. Coastal Zone and Estuarine Studies Division, NMFS, NOAA. Report to BPA, Contract No. DE-A179-83BP-39645.
- Murdoch, W.W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr. 39: 335-354.
- the development response of predators to changes in prey density. Ecology 52: 132-137.
1973. The functional response of predators. J. Appl. Ecol. 10: 335-342.
- Murdoch, W.W., and A. Oaten 1975. Predation and population stability, 1-131. In A. MacFayden. Advances in ecological research. Vol. 9. Academic Press.
- Neave, F. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. J. Fish. Res. Board Can. 9: 450-491.
- Noy-Meir, I. 1975. Stability of grazing systems: an application of predator prey graphs. J. Ecol. 63: 459-483.
- NPPC. 1986a. Technical discussion paper - Columbia River Basin fishery model. Northwest Power Planning Council, Portland, OR
- 1986b. Council and staff compilation of information on salmon and steelhead losses in the Columbia Basin. Northwest Power Planning Council, Portland, OR
1987. Columbia River Basin Fish and Wildlife Program. Adopted November 15, 1982, amended October 10, 1984, and February 11, 1987. Northwest Power Planning Council, Portland, OR.

- Olney, F.E. 1975. Life history of northern squawfish, Ptychocheilus oregonensis (Richardson), in Lake Washington. M.S. thesis. University of Washington. Seattle, WA.
- Paine, R.T. 1966. Food web complexity and species diversity. Am. Naturalist 100: 65-75.
- Patten, B.G., and D.T. Rodman. 1969. Reproductive behavior of the northern squawfish, Ptychocheilus oregonensis. Trans. Am. Fish. Soc. 98: 108-111.
- Peterman, R.M. 1977. A simple mechanism that causes collapsing stability regions in exploited salmonid populations. J. Fish. Res. Board Can. 34: 1130-1 142.
- Peterman, R.M., and M. Gato. 1978. Estimation of functional responses of predators on juvenile salmon. J. Fish. Res. Board Can. 35: 797-808.
- Poe, T.P., H.C. Hansel, S. Vigg, L.A. Prendergast, and D.E. Palmer. 1988. Predation of resident fish on juvenile salmonids in a mainstem Columbia River reservoir: Part I. Feeding ecology of northern squawfish, walleye, smallmouth bass, and channel catfish. in T.P. Poe and B.E. Rieman (eds.) Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-1986. Final Report, (Contracts DE-A179-82BP34796 and DE-A179-82BP35097) Bonneville Power Administration, Portland, OR.
- Raymond, H.D. 1969. Effect of John Day Reservoir on the migration rate of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. Trans. Am. Fish. Soc. 108: 505-529.
- Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board. Can. 11: 539-623.
- Rieman, B.E., R.C. Beamesderfer, L.J. Bledsoe, S. Vigg, and T. P. Poe. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: Part IV. Total loss and mortality caused by northern squawfish, walleye, and smallmouth bass. in T.P. Poe and B.E. Rieman (eds.) Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-1986. Final Report (Contracts DE-A179-82BP34796 and DE-A179-82BP35097) Bonneville Power Administration, Portland, OR.

- Ricker, W.E. 1941. The consumption of young sockeye salmon by predaceous fish. J. Fish. Res. Board Can. 5: 293-313.
1962. Regulation of the abundance of pink salmon populations. P. 155-211. In N.J. Wilimovsky (ed.) Symposium on pink salmon. Inst. Fisheries, University of British Columbia, Vancouver, B.C. Canada.
- Ruggerone, G.T. 1986. Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. Trans. Am. Fish. Soc. 115: 736-742.
- Ruggerone, G.T., and D.E. Rogers. 1984. Arctic char predation on sockeye salmon smolts at Little Togiak River, Alaska. Fish. Bull. 82: 401-410.
- Runge, J.A. 1980. The effects of hunger and season on the feeding of Calanus pacificus. Limnol. Oceanogr. 25: 134-145.
- Solomon, M.E. 1949. The natural control of animal populations. J. Anim. Ecol. 18: 1-35.
- Stewart, D.J., J.F. Kitchell, and L.B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans. Am. Fish. Soc. 110: 751-763.
- Stone, L. 1898. The salmon fisheries of the Columbia River, P. 801-823. In Report of the U.S. Bureau of Fisheries, 1875-1876, Washington, D.C.
- Swenson, W.A. 1972. Food competition between walleye, Stizostedion vitreum vitreum (Mitchell) and sauger, Stizostedion canadense (Smith), in Lake of the Woods, Minnesota. Ph.D. thesis. University of Minnesota. St. Paul, MN.
1977. Food consumption of walleye (Stizostedion vitreum vitreum) and sauger (S. canadense) in relation to food availability and physical environmental conditions in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. J. Fish. Res. Board Can. 34: 1643-1654.

- Taylor, R.J. 1977. The value of clumping to prey: experiments with a mammalian predator. *Oecologia* 30: 285-294.
1984. Predation. Chapman and Hall Ltd., London and New York. 166 p.
- Thompson, R.B. 1959. Food of the squawfish, Ptychocheilus oregonensis (Richardson), of the lower Columbia River. U.S. Fish Wild. Serv., Fish. Bull. 60: 43-58.
- Tinbergen, L. 1960. The natural control of insects in pinewoods. I. factors influencing the intensity of predation by songbirds. *Arch. Neerl. Zool.* 13: 266-336.
- Trefethen, P. 1972. Man's impact on the Columbia River, P 77-99. In R.T. Oglesby, C.A. Carlson, and J.A. McCann. River ecology and man. Academic Press, New York and London.
- Valiela, I. 1984. Marine ecological processes. Springer-Verlag, New York, 546 p.
- Vigg, S., and L.A. Prendergast. In Preparation. Gonad development and spawning of northern squawfish in a mainstem Columbia River Reservoir. Unpublished manuscript.
- Vondracek, B. 1987. Digestion rates and gastric evacuation times in relation to temperature of the Sacramento squawfish, Ptychocheilus grandis. Fish. Bull. 85:159-163.
- Walters, C.J., R. Hilborn, R.M. Peterman, and M.J. Staley. 1978. Model for examining early ocean limitation of Pacific salmon production. J. Fish. Res. Board Can. 35: 1303-1315.
- Ware, D.M. 1971. Predation by rainbow trout (Salmo gairdneri): the effect of experience. J. Fish. Res. Board Can. 28: 1847-1852.
1972. Predation by rainbow trout (Salmo gairdneri): the influence of hunger, prey density, and prey size. J. Fish. Res. Board Can. 29: 1193-1201.

Wood, C.C., and C.M. Hand. 1985. Food-searching behavior of the common merganser (Mergus merganser) I: Functional response to prey and predator density. Can. J. Zool. 63: 1260-1270.

Zaret, T.M., and T.R. Paine. 1973. Species introduction in a tropical lake. Science 182: 449-445.

SECTION II
Introduction
Oregon Department of Fish and Wildlife
Project No. 82-12
Contract No. DE-AI79-84BP35097

In 1982 the Bonneville Power Administration funded research on predation of juvenile salmon and steelhead. The goal of the work was to estimate the number and mortality of juvenile salmonids lost to resident fish predators in John Day Reservoir (see Executive Summary). We chose to estimate the loss directly by combining estimates of predator numbers and prey consumption rates. Because of the difficulty and complexity of estimating biological variables in a large reservoir such as John Day Reservoir we broke the problem into two parts. U.S. Fish and Wildlife Service described prey consumption. Oregon Department of Fish and Wildlife described the predator populations and combined predator population and prey consumption data to estimate juvenile salmonid loss and mortality.

As a biological process, predation is dynamic. An understanding of the variation in and the factors influencing mortality could benefit planning and management of salmon and steelhead. Variation in number and structure of predator populations, predator distribution, prey number and availability, and flow and temperature will affect the distribution of losses. To provide a better picture of predation we described the predator distribution, predator population dynamics, and predator-prey system dynamics. The papers in this section summarize our work. In the first two papers we address questions about the natural variation in predation by describing predator distribution, stratifying the loss estimates in time and space, and estimating the variance in the loss and mortality estimates. We used simulations to provide detail about the kind of annual variation expected in predator populations and about the changes in predation expected from direct manipulation of predators. We also used simulations to describe variation in predation expected with changes in prey number, temperature, and flow. The third and fourth papers summarize our results on predator population dynamics and predation. The fifth paper documents a model integrating available information on the predator-prey system and describes the variation expected in predation from variation in temperature, flow, prey numbers, predator numbers and travel time.

The results presented in this report represent a project that evolved over 5 years. In the first year, our work focused near the John Day and McNary dams (forebay and tailrace) under the assumption that most predation occurred in these areas. Early in the project we recognized that substantial predation also took place in the reservoir and expanded our efforts in following years. Initially, we concentrated work on two predators, walleye and northern squawfish, but expanded the work to include smallmouth bass and channel catfish later in the project. We did not obtain enough information to make a reasonable estimate of channel catfish abundance, and our results are limited to the first three species. The papers in this section present our

final results. However, for a more detailed review of the project evolution, the sampling design, intermediate data analysis, and data summaries we refer readers to the annual progress reports from this project (Nigro₁ et al. 1985; Nigro₂, et al. 1985; Nigro₃, et al. 1985; Willis et al. 1985; Beamesderfer et al. 1987; Rieman et al. 1987).

We did much work to develop methods or tools for analyses and interpretation of our data. We also used available information to look at questions important to future sampling. We provide documentation of the additional work in the supplement to this report. In the supplement the first paper describes results of a radiotelemetry study of the effects of variation in flow on distribution of northern squawfish in the McNary Dam tailrace. The second paper documents size selectivity of our sampling gear. Estimates of size selectivity were necessary to correct sample data used to describe population dynamics and to make population estimates. The third and fourth papers document simulation models MDCPOP and RESPRED used in the analyses described in our primary papers.

All project data in raw and summarized form is stored on magnetic tape with the Bonneville Power Administration. The supplement summarizes the data storage system and describes the format and codes necessary to access the data files.

References

- Beamesderfer, R.C., B.E. Rieman, J.C. Elliott, A.A. Nigro, and D.L. Ward. 1987. Distribution, abundance, and population dynamics of northern squawfish, walleye, smallmouth bass, and channel catfish in John Day Reservoir, 1986. Report (Contract DE AI79-82BP35097) to the Bonneville Power Administration, Portland, Oregon.
- Nigro₁, A.A., R.C. Beamesderfer, J.C. Elliott, M.P. Faler, L.M. Miller, and B.L. Uremovich. 1985. Abundance and distribution of walleye, northern squawfish, and smallmouth bass in John Day Reservoir, 1984. Report (Contract DE AI79-82BP35097) to the Bonneville Power Administration, Portland, Oregon.
- Nigro₂, A.A., R.C. Beamesderfer, J.C. Elliott, M.P. Faler, L.M. Miller, B.L. Uremovich, and D.L. Ward. Abundance and distribution walleye, northern squawfish, walleye, and smallmouth bass in John Day Reservoir, 1985. Report (Contract DE AI79-82BP35097) to the Bonneville Power Administration, Portland, Oregon.
- Nigro₃, A.A., C.F. Willis, R.C. Beamesderfer, J.C. Elliott, and B.L. Uremovich. 1985. Abundance and distribution of walleye, northern squawfish, and smallmouth bass in John Day Reservoir, 1983. Report (Contract DE AI79-82BP35097) to the Bonneville Power Administration, Portland, Oregon.

- Rieman, B. E. , R. C. Beamesderfer, A.A. Nigro, S. Vigg, H.C. Hansel, and D.E. Palmer. 1987. Preliminary estimates of loss of juvenile anadromous salmonids to predators in John Day Reservoir and development of a predation model. Report (Contract DE AI79-82BP35097) to the Bonneville Power Administration, Portland, Oregon.**
- Willis, C.F., A.A. Nigro, B.L. Uremovich, J.C. Elliott, and W.J. Knox. 1985. Abundance and distribution of walleye, northern squawfish, and smallmouth bass in John Day Reservoir, 1982. Report (Contract DE AI79-82BP35097) to the Bonneville Power Administration, Portland, Oregon.**

Predation by Resident Fish on Juvenile Salmonids in a Mainstem
Columbia Reservoir: Part III. Abundance and Distribution of
Northern Squawfish, Walleye, and Smallmouth Bass

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ABSTRACT

We used mark-recapture and catch-per-unit effort data to estimate abundance and distribution of three potential predators on juvenile salmonids migrating through John Day Reservoir, 1984-86. Northern squawfish *Ptychocheilus oregonensis* were the most abundant of the three (85,316), followed by smallmouth bass *Micropterus dolomieu* (34,954) and walleye *Stizostedion vitreum vitreum* (15,168). Because of uncertainty in sampling and assumptions of the mark-recapture estimator, the combined abundance of these three predators could range between 50,000 and 500,000 on a worst case. We believe, however, that bias is probably negative, and any errors should result in conservative estimates. Northern squawfish were common reservoir-wide but large concentrations were seen in the boat-restricted-zone immediately below McNary Dam. Walleye were largely restricted to the upper third of the reservoir, whereas the number of smallmouth bass increased progressively downriver. Some monthly and annual differences in distribution patterns were observed. Based on abundance and distribution, northern squawfish have the greatest potential for predation. We would also expect predation to be unevenly distributed in time and space based on variation in predator number and distribution.

Survival of young salmon and steelhead migrating through large mainstem reservoirs on the Columbia River is poor (Raymond 1979; Raymond 1988). For instance, as many as 20% of the 20 million salmon and steelhead entering John Day Reservoir annually are lost for unknown reasons (Sims and Ossiander 1981). This and similar unexplained mortality in a series of reservoirs substantially reduces production of adults (Raymond 1979). Predation by resident fishes was a suspected source of this mortality (Mullan 1980; Uremovich et al. 1980). Our goal was to estimate the magnitude of predation and to determine if predators accounted for a significant portion of the unexplained mortality (Rieman et al. 1988).

To determine whether predators were a significant source of mortality, we needed estimates of the abundance of predators. However, absolute estimates of abundance are often difficult to obtain (Everhart et al. 1975). Direct counts are possible only in exceptional circumstances such as where small water bodies can be drained, where clear water allows direct observation, or where spawning fish move past points of high visibility or catchability. In large systems estimates must be based on indirect techniques such as mark-recapture sampling (Everhart et al. 1975). Mark-recapture methods can be effective, but rely on a series of assumptions regarding population closure, mixing of marked and unmarked fish, etc. (Ricker 1975; Seber 1982). These assumptions introduce uncertainty into estimates of abundance in addition to the uncertainty related to sample sizes (Robson and Regier 1971; White et al. 1982). The uncertainty that results from assumptions is typically ignored in applications of estimates made from mark-recapture data (Ebener and Copes 1985; Neves et al. 1985; Slaney and Martin 1987) but could be important when making decisions based on estimates. On the Columbia River, an estimate of this uncertainty could help policy makers determine if evidence warrants a potentially expensive program for reducing predation.

To determine the magnitude of predation, we also needed information on the distribution of predators. Information on absolute abundance alone is insufficient for characterizing a population in a large reservoir. Large scale environmental patterns in large reservoirs may result in uneven patterns of distribution (King et al. 1981). Large areas of unsuitable habitat may be uninhabited by predators. Vulnerability of prey to predators may also vary with habitat. Prey consumption by predators may be low despite large predator populations if prey find refuges where no predators occur or where vulnerability to predation is reduced. Patterns of distribution may also be variable, changing with season, year or fish size. Failure to identify these distribution patterns could lead to erroneous interpretation of abundance information.

Finally, we needed information on predator consumption rates to estimate the magnitude of predation. Vigg et al. (1988) detail sampling efforts to measure these consumption rates in the field and Rieman et al. (1988) incorporate those field estimates with abundance and distribution information from our paper to calculate an estimate of salmonid losses and mortality. The objectives of this paper are: (1) estimate predator abundance so that prey loss and mortality could be calculated with additional information on individual consumption rates; (2) determine uncertainty in estimates of abundance based on sampling variability and uncertainty resulting from our use of mark-recapture estimators; (3) estimate the distribution of predators.

STUDY AREA

John Day Reservoir (Lake Umatilla) is one of a series of impoundments operated for hydroelectric power generation, navigation, and flood control on the lower Columbia River between Oregon and Washington. The reservoir is 123 km long, up to 3.5 km wide and has a surface area of about 20,000 hectares. The reservoir is bounded by John Day (RKM 348) and McNary (RKM 471) dams. John Day Reservoir includes a variety of habitats. The upper section of the reservoir is riverine and contains numerous islands and shallow embayments. Depth averages 10 m. The lower reservoir is more lotic, has steep shorelines, and has little littoral zone. Depth ranges up to 50 m.

A variety of fishes occur in John Day Reservoir (Hjort et al. 1981; Poe et al. 1988). Salmonids including steelhead *Salmo gairdneri*, chinook salmon *Oncorhynchus tshawytscha*, sockeye salmon *Oncorhynchus nerka*, and coho salmon *Oncorhynchus kisutch* spawn in, rear in, or migrate through the reservoir. Numbers of salmonids are highest during the period of smolt migration from April through August. The predominant resident piscivores appear to be northern squawfish *Ptychocheilus oregonensis*, walleye *Stizostedion vitreum vitreum*, smallmouth bass *Micropterus dolomieu*, and channel catfish *Ictalurus punctatus*.

METHODS

Field Sampling

We sampled John Day Reservoir from April through August, 1982-86, to describe the abundance and distribution of northern squawfish, walleye, and smallmouth bass. We also collected channel catfish but were unable to sample enough to produce reasonable estimates of abundance and distribution. In 1982 we surveyed the reservoir and established sampling methods. In 1983 we increased our effort and refined our methods. From 1984 through 1986, we conducted similar full scale sampling efforts. Effort was equally partitioned into two-week intervals throughout the period of sampling.

We sampled primarily in five areas of the reservoir: Immediately above John Day Dam (forebay), Arlington, Irrigon, McNary Dam tailrace, and the boat-restricted zone (BRZ) below to McNary Dam (Figure 1). We allocated equal effort to each area except the BRZ, which we sampled less because of its small size. Sampling areas ranged in length from 0.6 to 15 km and were selected to represent the range of habitats available in the reservoir. Sampling sites within areas were selected to cover each area and to maximize catch. Sites were fixed and were sampled during each two-week period. We also sampled with limited effort in Rock Creek and Crow Butte areas of the reservoir in 1985 and 1986 (Figure 1).

Fish were collected with (1) two types of monofilament gillnets (46 m long by 2.4 m deep with alternating panels of 3.2, 4.4, and 5.1 cm bar mesh; 46 m long by 2.4 m deep with alternating panels of 6.4 and 7.6 cm bar mesh); (2) Lake Erie style trapnets (61 m long by 3.1 or 4.6 m deep with leads of 3.2 or 3.8 cm bar mesh); (3) electrofishing boats; and (4) hook-and-line from John Day and McNary Dams. Gear was deployed for standardized periods of time: 1 hour for gillnet and angling, 24 hours for trap nets, and 900-seconds current

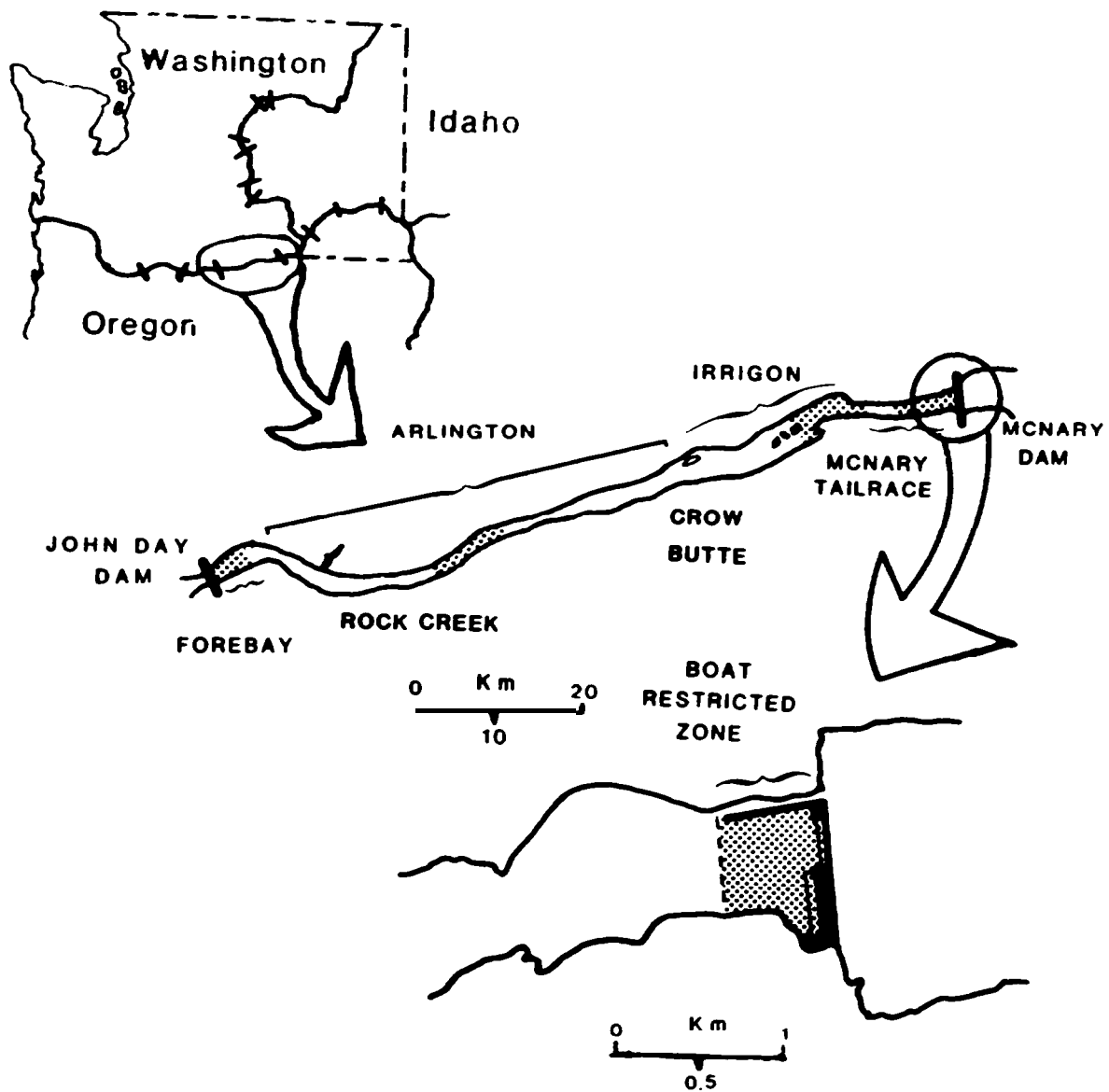


Figure 1. Sampling areas (shaded) and areas assumed to be represented by sampling (in brackets) in John Day Reservoir 1984, 1965, and 1986.

on time for electrofishers. We sampled primarily at night, near shore. We attempted to find a method of sampling offshore but were unsuccessful. Current velocity, depth, irregular bottom contours, barge traffic, and apparent low densities of fishes made sampling with vertical gillnets, drift gillnets, sinking gillnets, electrofishers, box traps, and otter trawls unproductive.

All fish caught were identified and counted. Fork lengths (mm) and weights (g) of northern squawfish, walleye, and smallmouth bass were measured. Fish that were bleeding excessively or unable to maintain equilibrium were killed. Northern squawfish and walleye with fork lengths of 250 mm or greater and smallmouth bass with fork lengths of 200 mm or greater were marked with numbered spaghetti tags inserted through dorsal musculature and tied over the back with an overhand knot. Fish were secondarily marked with opercle punches or pelvic fin clips.

Samples were supplemented by fish tagged and released in concurrent sampling by the U.S. Fish and Wildlife Service (FWS) (Poe et al. 1988). FWS provided records of their catch and recover of marked fish.

We also interviewed anglers for catch rate and catch composition information and counted anglers to estimate total effort (Olson et al. 1988). Angler surveys were conducted each weekend day and on two of every five week days concurrent with other field sampling. Angler surveys were conducted in McNary tailrace in 1983 and 1984 and were expanded to include John Day forebay and river in 1985 and 1986. Voluntary returns of tags by anglers were solicited throughout the reservoir with posters and drop boxes.

In addition, we monitored movements of radiotagged northern squawfish and walleye in 1985 (Nigro₁ et al. 1985). Radio transmitters were surgically implanted into 23 northern squawfish and 20 walleye prior to the start of sampling. Fish were located from airplane, boat, and shore at 3 or 4 day intervals throughout the period of field sampling.

Abundance

Abundance of northern squawfish, walleye, and smallmouth bass was estimated each year from 1984 through 1986 using a multiple mark and recapture method (Seber 1982). Overton's modification of the Schnabel estimator was used to account for natural and fishing mortality and fish that were killed during sampling (Overton 1965). Mark-recapture samples were grouped by two-week periods. Fish recaptured in the same period in which they were marked were not treated as recaptures for estimation purposes. Estimates from each year were compared statistically ($P \leq 0.05$) with 1986 estimates using a test for differences between Schnabel estimates (Chapman and Overton 1966) to determine if abundance was constant throughout the study. Because of concerns about partial mixing of marked and unmarked northern squawfish and walleye, we also made Petersen-type estimates (Seber 1982) of their abundance using recoveries from the year following the year of marking. We assumed the longer period between marking and recovery periods would allow more complete mixing.

Estimates of abundance based on Overton's estimator incorporated various corrections to minimize bias that results from violations of assumptions of the estimator. The validity of each assumption was independently evaluated to determine if and to what degree corrections were warranted. Mark-recapture assumptions that were considered included (1) closure of the population to recruitment and mortality, (2) mixing of marked and unmarked fish, (3) equal vulnerability to capture of all fish in the population, (4) equal catchability of marked and unmarked fish, and (5) recognition of all marked fish at recapture (Ricker 1975; Seber 1982).

In addition to "best guess" estimates corrected for violations of assumptions, we also made alternative estimates using a range of corrections to determine sensitivity to each assumption. We used these alternatives to determine the size and direction of bias in estimates of abundance if our independent assessment of violation and corresponding correction were incorrect.

The assumption that populations were closed to recruitment was examined with respect to growth of fish into the "tagable" size range during sampling. The minimum size of fish included in estimates was adjusted midway through the sampling season to correct the abundance estimate for growth during sampling. Size of fish during sampling was adjusted by half the observed average annual increment (Rieman et al. 1988) because our sampling season represented most of the growing season. Effects of this assumption were examined with alternative estimates made using growth equal to zero and to the full annual increment.

The assumption that populations were closed was also examined with respect to removals by anglers. Angler harvest was estimated as the product of effort estimated from counts of anglers and catch per unit effort estimated from angler interviews (Olson et al. 1988). Harvest of marked fish was also estimated from voluntary tag returns by anglers assuming a 50% nonreturn rate (Rieman 1987). The larger of the two estimates in each two-week period was used to adjust abundance estimates. Thus, estimates for northern squawfish, walleye, and smallmouth bass were corrected for exploitation rates of 2%, 0%, and 20%, respectively. Adjustments for observed and alternative estimates of exploitation were made using Overton's modification of the Schnabel estimator (Overton 1965).

We examined the assumption that marked and unmarked fish mix throughout the population by looking at movements of marked and radiotagged fish. Mixing was assumed to be complete where frequent movements among our sampling areas were observed and where large distances were traveled in a period of two weeks or less. No mixing was assumed where fish were seldom recaptured in sites or areas other than where released. Complete mixing was assumed for northern squawfish because 70% of recaptures from 1984 to 1986 were in sites other than where released, 35% of all recaptures were outside the area of release, ranges of radiotagged northern squawfish averaged 30 river km in length, and radiotagged northern squawfish moved an average of 0.23 km/day. Complete mixing was also assumed for walleye throughout the upper reservoir because 68% of recaptures were in sites other than where released, 21% of all recaptures were in areas outside the area of release, ranges of radiotagged walleye averaged 49 river km in length, and radiotagged walleye moved an average of 0.3 km per day. We assumed mixing of walleye was complete only through June because many of our radiotagged walleye remained outside sampling

areas after June. We assumed no mixing of marked smallmouth bass beyond sampled areas because only 30% of all recaptures were at sites other than where released and only 5% were in other sampling areas.

To accommodate the assumption of complete mixing in the estimate of abundance, samples from all areas were pooled and a single estimate was calculated. The opposite case (no mixing) was approximated by expanding area-specific estimates according to relative sizes of sampled and unsampled areas. Area-specific estimates of abundance were also summed without expansion for unsampled areas to approximate a situation of incomplete mixing where fish moved into areas adjacent to sampled areas but zones of mixing did not overlap. Seasonal changes in the degree of mixing were accommodated by restricting the duration of the mark-recapture experiment to periods when fish mixed. Peterson estimates also addressing the assumption of mixing. We assumed Peterson estimates would be larger than multiple mark and recapture estimates if short-term mixing was incomplete.

The assumption that all fish in the population were equally vulnerable to capture was examined with respect to size selectivity of our combined gear. Size selectivity was described with recapture-at-large ratios and significant size differences were identified with chi-square tests (Beamesderfer and Rieman in press). Abundance estimates may be corrected for differential vulnerability by making separate estimates for size classes of similar vulnerability (Ricker 1975). However, splitting the population results in a reduction in precision of estimates (Seber 1982). We observed size selectivity in our sampling for all species (Beamesderfer and Rieman In press) but did not make corrections in our "best" estimates of abundance because the loss of precision when samples were split was greater than the bias that resulted from size selectivity in the pooled sample.

The assumption that marked and unmarked fish were equally vulnerable to capture was examined with respect to mortality that resulted from capture and handling. Mortality following release was investigated by holding fish for 3 days (Nigro₂ et al. 1985). We assumed no mortality of marked fish in any of the three populations we examined because we saw no mortality among fish that appeared in good condition following marking. Only fish in obviously poor condition at capture died, so we assumed that limiting marking to fish in good condition minimized mortality after release. Effects of mortality of marked fish were examined by reducing the at-large number of tags proportionate to increases in mortality.

The assumption that all marked fish were recognized at recapture was examined with respect to tag loss, which was identified from secondary marks. Although we observed losses of tags at rates ranging from 3% in smallmouth bass to 29% in northern squawfish, secondary marks and tag scars were readily apparent. We therefore assumed all marks were recognized because only trained personnel examined fish for tags. Effects of tag loss on estimates of abundance were examined by adding the numbers of tags lost to the number of recaptures.

Distribution

We described the relative distribution of predators by using catch per unit effort (CPUE). We assumed that CPUE was directly proportional to density. Relative density in each area was calculated by dividing CPUE of a gear in each area by the reservoir-wide total for that gear, then averaging the percentages for all gear. Gillnets, trap nets, and electrofishers were included for northern squawfish and walleye. Comparisons were limited to electrofisher catches for smallmouth bass because other gears were ineffective for that species. We treated each month separately to eliminate seasonal variation in gear-specific vulnerability. We treated two size classes separately to identify size differences in distribution. We made splits between classes where breaks in size selectivity of gear were observed (Beamesderfer and Rieman In press), or if no breaks were observed, where sample sizes in each class were equal.

CPUE of walleye and smallmouth bass was compared among four sampling areas (BRZ omitted). BRZ was included for northern squawfish because we observed unusually high CPUE in that area. Relative abundance in the BRZ was described using only differences in CPUE of electrofishers between the BRZ and the other four areas because electrofishers were the only gear used inside the BRZ.

CPUE among areas was compared statistically to separate inherent differences from those related to sampling error. Two-way analysis of variance (Neter et al. 1985) was used to identify significant ($P < 0.05$) differences in CPUE among sampling areas with gear type included as a blocking variable. One-way analysis of variance of electrofishing data was used to compare CPUE of northern squawfish in the BRZ with CPUE in other areas. Three-way analysis of variance were used to identify significant effects of size, month, and year on CPUE among areas. Observations were catches with gear deployed for a standard length of time. We transformed catch data ($\log [x + 1]$) to meet statistical assumptions (Moyle and Lound 1960; Elliott 1977). Observations were included for all fish greater than minimum tagable sizes, for months April through August and for years 1984-86.

Independent estimates of relative density in areas of the reservoir were made from observed frequencies of occurrence of radiotagged fish and from area specific abundance estimates divided by area sizes in hectares. Radiotelemetry information provided an alternative means of estimating distribution if radiotagged fish were representative of the population. This assumption was violated among northern squawfish because none from the midreservoir were radiotagged. Consequently, relative abundance estimates using radiotagged fish were made only for walleye. Area-specific estimates of abundance appeared to be appropriate only for smallmouth bass, which moved very little.

Inshore and offshore patterns of distribution were described using observations of radiotagged northern squawfish and walleye. Observations within 50 m of shore were classified as inshore. Relative frequencies were compared among months to identify seasonal changes in inshore-offshore distribution. Chi-square tests (Steel and Torrie 1980) were used to determine whether monthly differences were significant ($P < 0.05$).

RESULTS

Northern Squawfish

Abundance

Average abundance of northern squawfish in John Day Reservoir from 1984-86 was estimated at 85,316 fish (4.4 per hectare) larger than 250 mm in length based on the multiple mark and recapture estimator. Only the estimate from 1984 was significantly different ($P \leq 0.05$) from the 1986 estimate although estimates have increased 15%-20% each year 1984 through 1986 (Table 1). Average confidence intervals ranged from -23% to +28%. Estimates of the number of northern squawfish based on a single mark-and-recovery estimator were similar in size to those calculated with the multiple mark-and-recapture estimator (Table 1).

Table 1. Number of northern squawfish exceeding 250 mm in length in John Day Reservoir, 1983-86, and results of statistical tests for differences from the 1986 estimate.

Year	Multiple mark and recapture				Single mark and recapture		
	Estimate of abundance (<i>p</i>)	95% confidence limits			Estimate of abundance	95% confidence limits	
		Lower	Upper			Lower	Upper
1983		--	--		87,700	70,264	105,136
1984	68,947 (0.03)	55,250	86,040		75,732	61,330	90,134
1985	84,114 (0.23)	66,905	105,749		109,399	86,339	132,459
1986	102,888 --	75,215	136,059		--	--	

Our estimate of the abundance of northern squawfish was sensitive to the assumptions used in the estimator (Table 2). The estimate was most sensitive to assumptions of the degree of mixing of marked fish throughout the reservoir and least sensitive to assumptions of growth during sampling and removals by anglers in the ranges we observed. The direction of bias that resulted from violations of assumptions also varied. For instance, underestimation of angler harvest, of the degree of mixing and of differences in vulnerability of different sizes all led to underestimation of abundance. Underestimation of growth during sampling, of mortality of marked fish and of nonrecognition of marks lead to overestimation of abundance. Precision of the estimate was affected only by assumptions of mixing, vulnerability to capture and nonrecognition of marks.

Distribution

Indexes of relative density based on CPUE of three gears, indicated northern squawfish were not evenly distributed through the reservoir. The index in the BRZ (0.789) was 12-18 times higher than in other areas of the reservoir. Relative density was similar among areas outside the BRZ although densities in the forebay (0.066) and McNary Dam tailrace (0.055) appeared

Table 2. Alternatives estimates of the abundance of northern squawfish in 1986, based on violations of assumptions. Effects of violations on magnitude and precision of abundance estimate were calculated relative to an estimate based on assumption of zero violation.

Assumption, alternative	Estimate of abundance	Width of confidence limit ^a (%)
Growth during sampling:		
None	109,082	59
Half annual increment ^b	102,888	59
Full annual increment	94,227	60
Angler Harvest:		
0%	101,996	59
2% ^b	102,888	59
5%	105,187	59
10%	108,571	59
Mixing:		
Complete ^b	102,888	59
Nonoverlapping	219,128	220
None	490,540	290
Vulnerability:		
Equal ^b	102,888	59
Unequal (2 size groups)	127,732	87
Marked fish mortality:		
0% ^b	102,888	59
10%	92,961	59
50%	53,130	59
Nonrecognition of marks:		
0% ^b	102,888	59
10%	93,454	55
50%	52,895	40

^a Upper limit minus lower limit divided by estimate of abundance times 100.

^b Degree of violation incorporated in best estimate.

slightly higher than in Arlington (0.044) or Irrigon (0.044). Differences among areas were significant (Appendix Tables 1 and 2).

Distribution of northern squawfish was size-related. Relative densities of fish larger than 400 mm in the BRZ (0.900) were greater than those of fish in the 250-400 mm size range (0.715). Size differences in relative densities among reservoir areas were significant (Appendix Tables 1 and 2).

Seasonal changes in distribution of northern squawfish were found. Relative index of density in the BRZ increased from April through August (Figure 2). Density in McNary tailrace peaked in May and June. CPUE in Arlington and Irrigon declined as CPUE increased upriver. Month differences in relative densities among reservoir areas were significant (Appendix Tables 1 and 2).

We saw no obvious differences in distribution of northern squawfish among years although year effects on patterns of relative density between areas were significant (Appendix Tables 1 and 2). Densities were consistently highest in the BRZ and similar in all other areas (Table 3).

Table 3. Index of relative density of northern squawfish in areas of John Day Reservoir in three years, based on catch per unit effort.

Year	Forebay	Arlington	Irrigon	McNary	Boat-restricted-zone
1984	0.063	0.055	0.036	0.053	0.793
1985	0.069	0.036	0.054	0.066	0.775
1986	0.067	0.044	0.042	0.048	0.799

Northern squawfish were most likely to occur within 50 m of shore based on radiotelemetry observations (Table 4). Numbers observed inshore declined from April through August. Differences among numbers were significant ($P < 0.01$).

Table 4. Number of radiotagged northern squawfish observed in inshore (<50 m) and offshore areas of John Day Reservoir, 1984-85.

Area	April	May	June	July	August
Inshore	151	234	247	241	183
Offshore	8	27	51	118	79

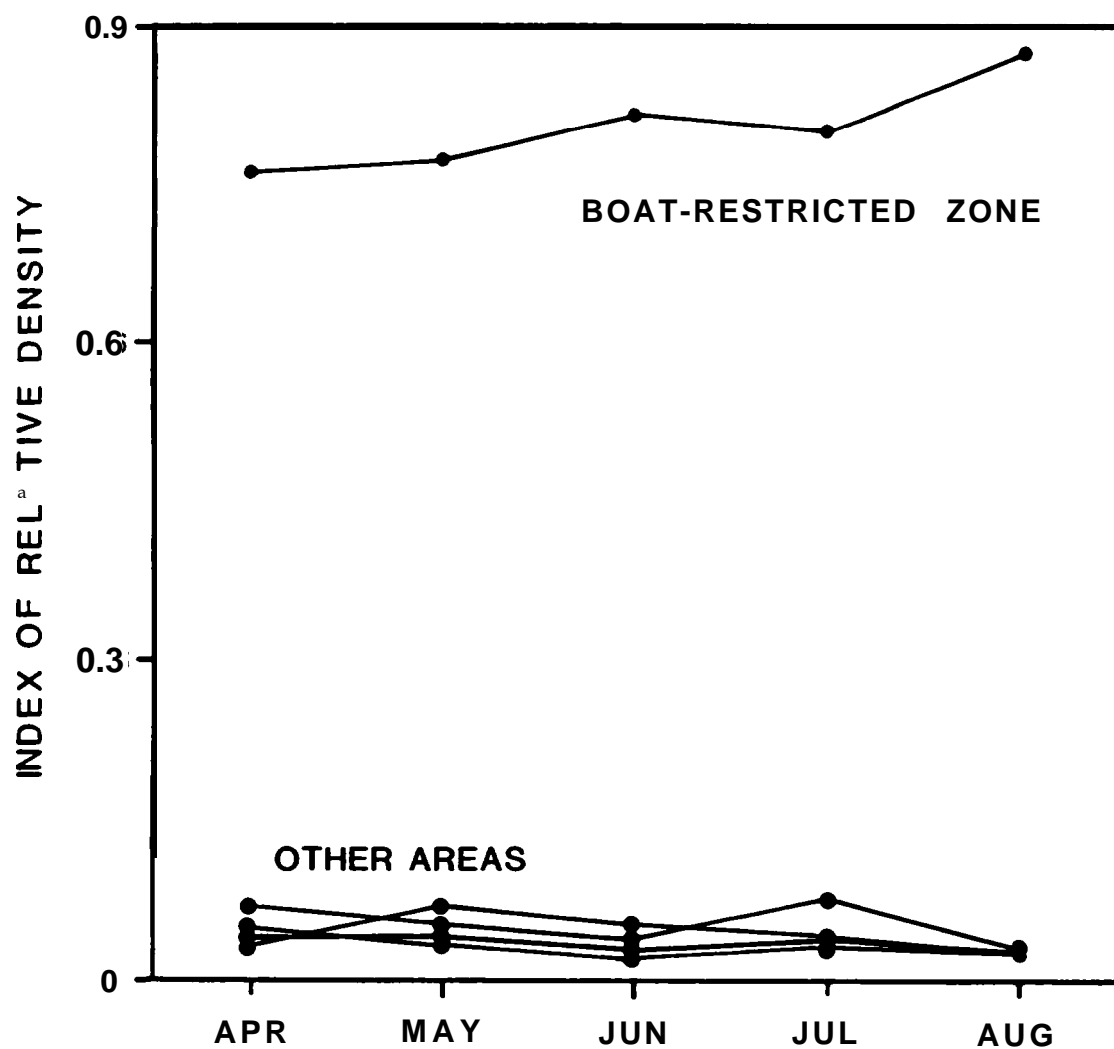


Figure 2. Index of relative density of northern squawfish in five areas of John Day Reservoir, April-August. Index is based on catch per unit effort in three gears of fish with fork lengths greater than 250 mm 1984-86.

Walleye

Abundance

Average abundance of walleye in John Day Reservoir from 1984 through 1986 was estimated at 15,168 fish larger than 250 mm in length (0.8 fish per hectare). Estimates from 1984 and 1985 were not significantly different ($P \leq 0.5$) from the 1986 estimate (Table 5). Average confidence intervals ranged from -60% to +117%. Estimates of walleye numbers based on a single mark-recapture estimator were less than those calculated with the multiple mark-recapture estimator (Table 5).

Table 5. Number of walleye exceeding 250 mm in length in John Day Reservoir, 1983-86, and statistical tests for differences from the 1986 estimate.

Year	Multiple mark and recapture			Single mark and recapture		
	Estimate of abundance (p)	95% confidence limits		Estimate of abundance	95% confidence limits	
		Lower	Upper		Lower	Upper
1982	--	--	--	7,610	4,470	10,750
1983		--	--	7,910	5,889	9,933
1984	13,042 (0.69)	6,573	23,006	9,681	6,747	12,615
1985	18,426 (0.87)	7,236	39,855	13,838	6,816	20,860
1986	14,036 (--)	4,520	36,003	--	--	--

Our estimate of walleye abundance was sensitive to violations of assumptions (Table 6). Assumptions of growth, angler harvest and vulnerability had minor effects on the estimate of abundance. Assumptions of marked fish mortality and nonrecognition of marks had greater effects. We were unable to assess the effect of alternative assumptions of mixing because recapture numbers were too small for anything other than a pooled-area estimate. Directions of biases were negative for assumptions of growth, vulnerability, marked fish mortality, and nonrecognition of marks. Bias was positive for an assumption of angler harvest. Precision of estimates was affected by assumptions of growth, vulnerability, and nonrecognition of marks.

Distribution

Walleye were unevenly distributed throughout John Day Reservoir. Indexes of relative density based on CPUE and radiotelemetry data indicate most walleye occur above Arlington (Figure 3). Walleye were rarely observed below Arlington. Area differences in relative density based on CPUE were significant (Appendix Table 3).

Table 6. Alternative estimates of walleye abundance in 1986, based on violations of assumptions. Effects of violations on magnitude and precision of abundance estimate were calculated relative to an estimate made based on an assumption of zero violation.

Assumption, alternative	Estimate of abundance	Width of confidence limit^a (%)
Growth during sampling:		
None ^b	14, 036	225
Half annual increment	12, 989	267
Full annual increment	12, 552	267
Angler harvest:		
0% ^b	14, 036	225
2%	14, 204	224
5%	14, 484	224
10%	14, 963	225
Mixing:		
Complete ^b	14, 036	225
Nonoverlapping ^c	--	--
None ^c	--	--
Vulnerability:		
Equal ^b	14, 036	225
Unequal (2 size groups)	13, 227	328
Marked fish mortality:		
0% ^b	14, 036	225
10%	12, 505	224
50%	7, 138	224
Nonrecognition of marks:		
0% ^b	14, 036	225
10%	11, 702	197
50%	7, 032	141

a Upper limit minus lower limit divided by estimate of abundance times 100.

b Degree of violation incorporated in best estimate.

c Unable to estimate because of limited recaptures.

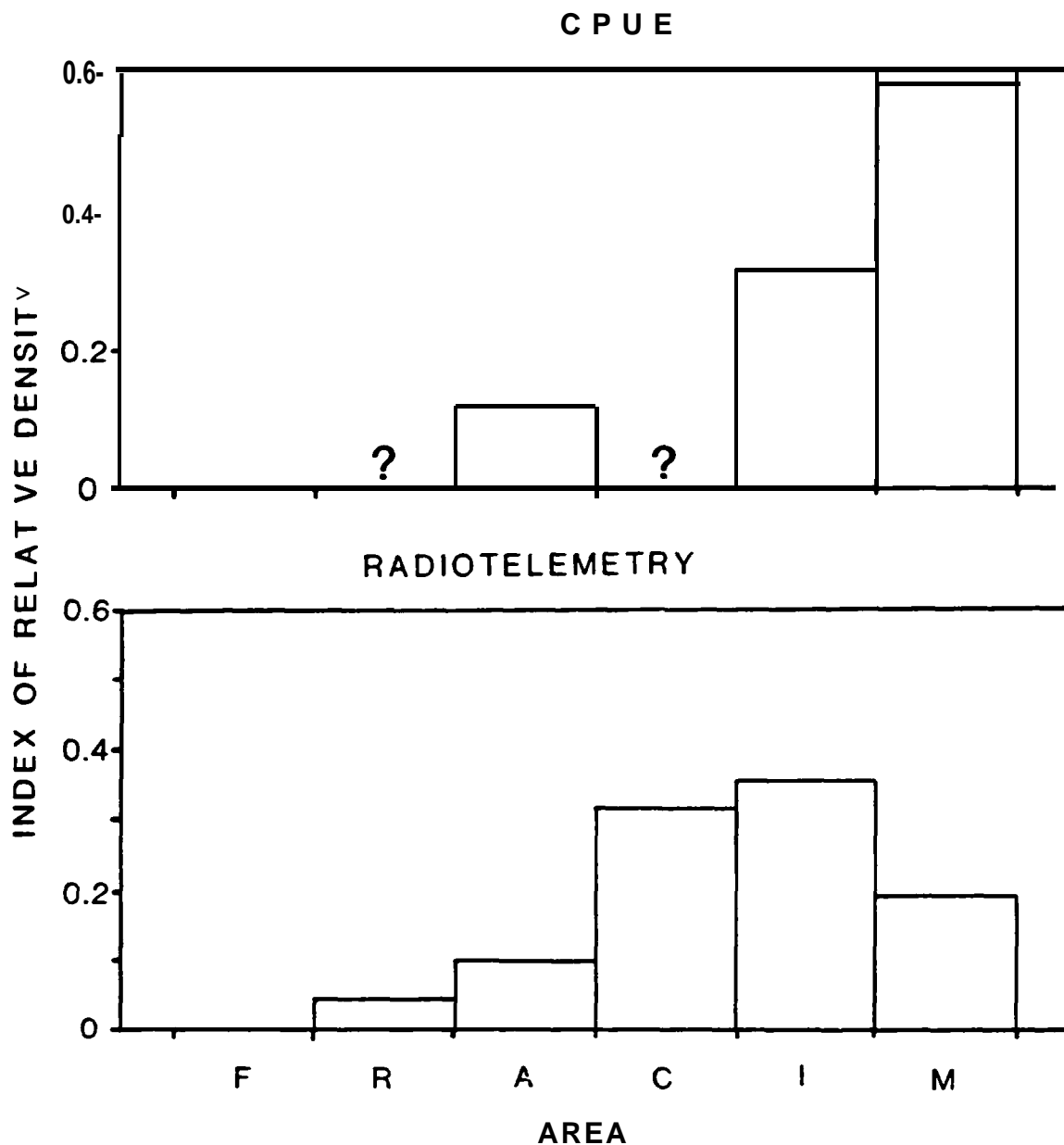


Figure 3. Index of relative density of walleye in six areas of John Day Reservoir. Index is based on catch per unit effort (CPUE) in three gears of fish with fork lengths greater than 250 mm in April through August, 1984-86, and also on proportions of radiotagged fish observed in each area in 1985. Areas include forebay (F), Rock Creek (C), Arlington (A), Crow Butte (C), Irrigon (I), and McNary tailrace (M).

Walleye distribution also varied with size of fish. Fish in the 250-500 mm size range were more likely to be found in McNary tailrace (index of relative density = 0.692) than were fish larger than 500 mm (index of density = 0.525). Size differences in relative densities among areas were significant (Appendix Table 3).

We observed distinct monthly changes in distribution of walleye. Density in April was highest in McNary tailrace and gradually declined from April through July as walleye appeared to redistribute down reservoir (Figure 4). Densities in McNary tailrace appeared to increase again in August but we suspect this to be an anomaly resulting from low catch rates reservoir-wide in August. Monthly differences in patterns of relative density between areas were significant (Appendix Table 3).

We saw slight differences in the distribution of walleye in John Day Reservoir among years. Walleye were more abundant outside McNary tailrace in 1985 than in 1984 and 1986 (Table 7). Differences between years were significant (Appendix Table 3). Annual variation in distribution may be explained by annual variation in environmental conditions. In 1985, temperature increased earlier than in 1984 and 1986 (Figure 5).

Table 7. Index of relative density of walleye in areas of John Day Reservoir based on catch per unit effort, 1984-86.

Year	Forebay	Arlington	Irrigon	McNary
1984	0	0.079	0.300	0.621
1985	0.006	0.124	0.372	0.498
1986	0	0.138	0.242	0.621

Walleye were most likely to occur within 50 m of shore but this tendency was reduced after June (Table 8). Differences in number inshore and offshore among months were significant.

Table 8. Number of radiotagged walleye observed in inshore (<50 m) and offshore areas of John Day Reservoir, 1984-85.

Area	April	May	June	July	August
Inshore	162	205	216	157	54
Offshore	60	66	61	131	62

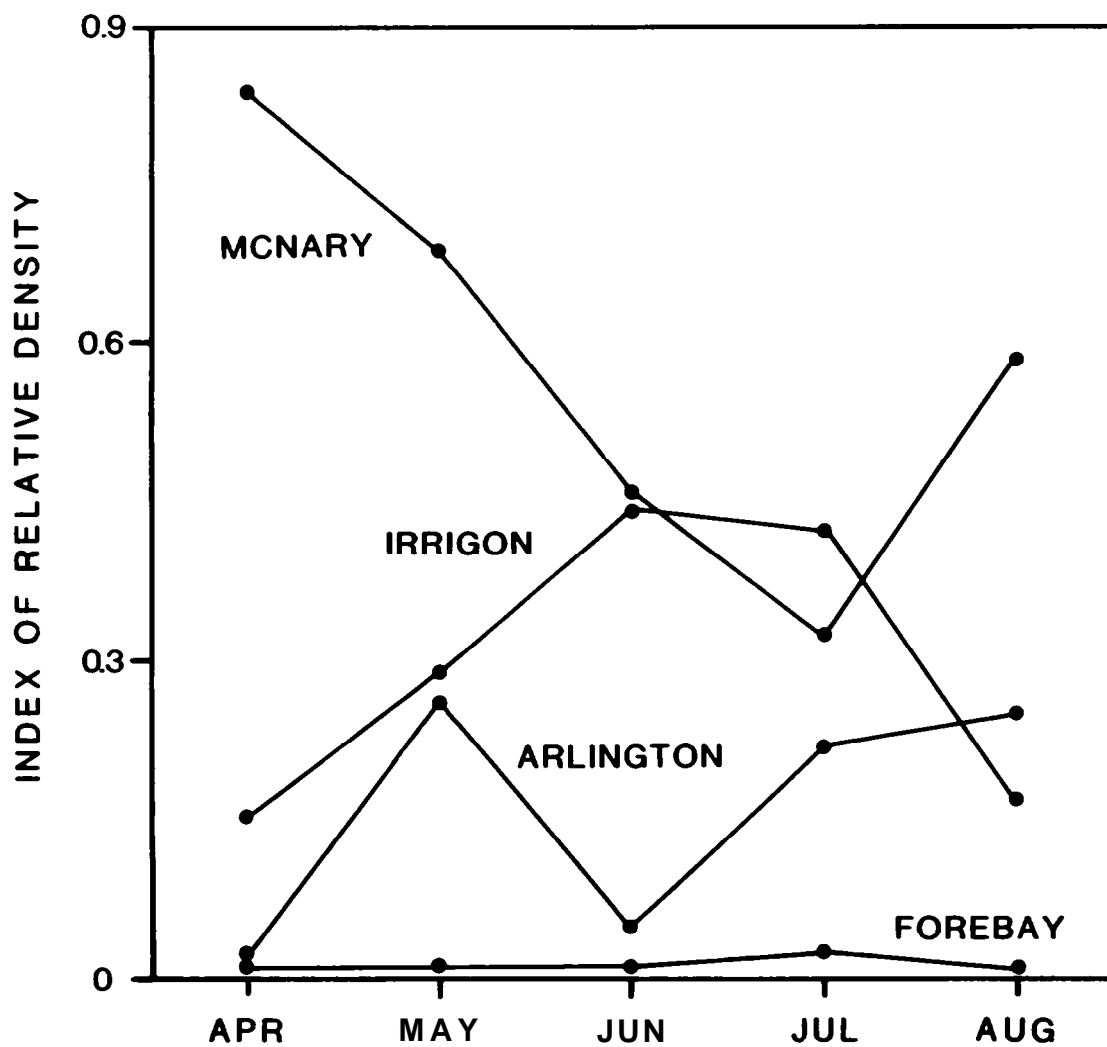


Figure 4. Index of relative density of walleye in four areas of John Day Reservoir, April-August. Index is based on catch per unit effort in three gears of fish with fork lengths greater than 250 mm 1984-86.

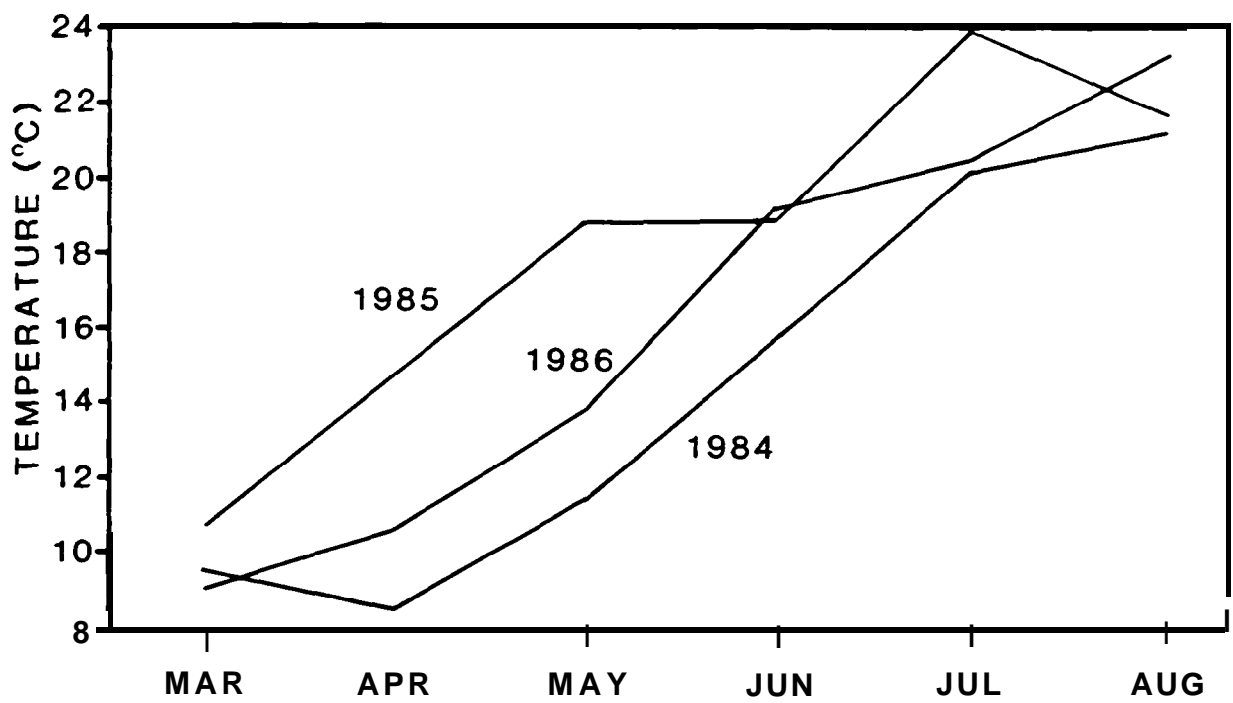


Figure 5. Monthly mean temperature in John Day Reservoir, 1984-86.

Smallmouth Bass

Abundance

Abundance of smallmouth bass averaged 34,954 fish 200 mm in length and greater (1.8 fish per hectare) in John Day Reservoir in 1985 and 1986. The 1984 estimate underestimated smallmouth bass abundance because sampling incompletely covered the reservoir and substantial harvest by anglers in the lower reservoir was ignored. Differences between estimates from 1985 and 1986 were probably not significant although statistical comparisons were not made (Table 9). Confidence intervals for estimates averaged $\pm 28\%$

Table 9. Number of smallmouth bass exceeding 200 mm in length in John Day Reservoir, 1983-86.

Year	Estimate of abundance	95% Confidence Limits	
		Lower	Upper
1984 ^a	13,352	10,933	15,771
1985	31,948	18,967	44,929
1986	37,959	29,019	46,899

a 1984 estimate was not adjusted for angler harvest in the lower reservoir and incompletely covered the Irrigon area.

Our estimate of abundance of smallmouth bass was sensitive to assumptions of growth during sampling, angler harvest, mixing, vulnerability, marked fish mortality, and nonrecognition of marks over the potential range of violation (Table 10). The most important assumption was that regarding mixing. An assumption of vulnerability had a several fold effect on precision. Precision was also affected by assumptions of mixing and nonrecognition of marks.

Distribution

Smallmouth bass were unevenly distributed in John Day Reservoir. Estimates of relative abundance from mark-recapture estimates of abundance expressed per unit of area and from CPUE indicate smallmouth bass were most abundant in John Day Forebay and least abundant in McNary tailrace (Figure 6).

The distribution of smallmouth bass among areas was size-related. Fish larger than 250 mm in length were evenly distributed throughout the reservoir except in McNary tailrace where smallmouth bass were uncommon. Density index varied from 0.300 to 0.324 outside McNary tailrace. The number of fish in the 200-250 mm size range was much higher in the forebay than elsewhere. In the forebay the density index was 0.479, whereas the index in Arlington was 0.240 and in Irrigon was 0.235. Size differences were significant (Appendix Table 4).

Table 10. Alternative estimates of smallmouth bass abundance in 1986, based on violations of assumptions. Effects of violations on magnitude and precision of abundance estimate were calculated relative to an estimate made based on an assumption of zero violation.

Assumption, alternative	Estimate of abundance	Width of confidence limit^a (%)
Growth during sampling:		
None	47,630	45
Half annual increment ^b	37,959	47
Full annual increment	31,745	48
Angler harvest:		
0%	30,113	45
10%	31,515	44
20% ^b	37,959	47
30%	35,666	45
50%	41,439	45
Mixing:		
Complete	14,428	33
Nonoverlapping	13,657	64
None ^b	37,959	47
Vulnerability:		
Equal ^b	37,959	
Unequal (2 size groups)	48,068	152
Marked fish mortality:		
0% ^b	37,959	47
10%	35,353	47
50%	24,095	48
Nonrecognition of marks:		
0% ^b	37,959	47
10%	35,535	45
50%	24,276	34

^a Upper limit minus lower limit, divided by estimate of abundance times 100.

^b Degree of violation incorporated in best estimate.

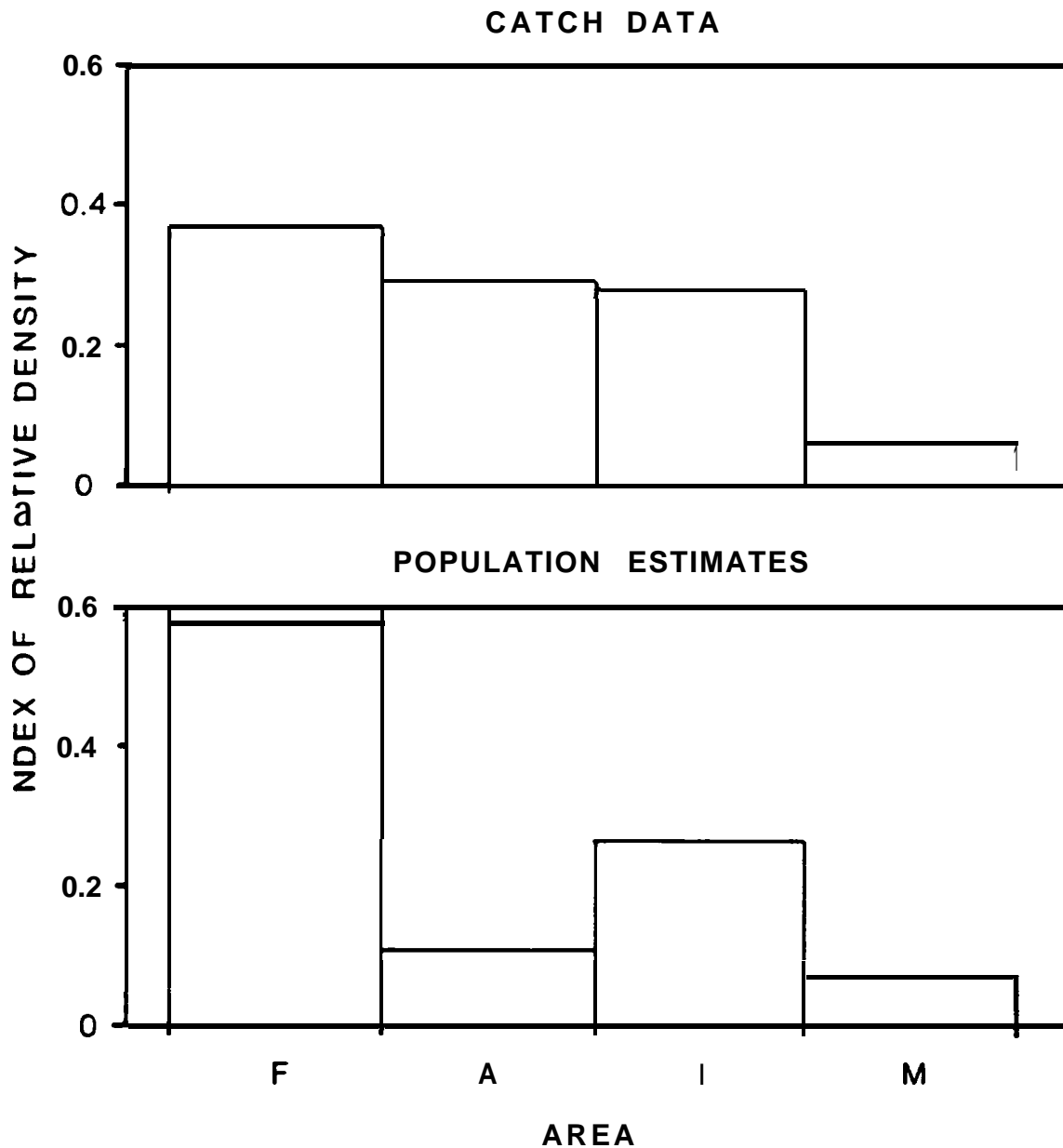


Figure 6. Index of relative density of smallmouth bass in four areas of John Day Reservoir. Index is based on catch per unit effort (CPUE) by electrofisher of fish with fork lengths greater than 200 mm from April through August, 1984-86, and also on proportions of total estimated abundance. Areas include forebay (F), Arlington (A), Irrigon (I), and McNary tailrace (M).

The distribution of smallmouth bass also appeared to change from month to month. Patterns in each month were generally similar with maximum densities in the forebay and minimum density in McNary tailrace (Figure 7). Differences in CPUE among months were significant (Appendix Table 4).

Relative density in the forebay, Arlington, and Irrigon varied from year to year (Table 11). Annual differences were significant (Appendix Table 4).

Table 11. Index of relative density of smallmouth bass in areas of John Day Reservoir, based on catch per unit effort, 1984-86.

Year	Forebay	Arlington	Irrigon	McNary
1984	0.457	0.298	0.227	0.018
1985	0.372	0.303	0.285	0.040
1986	0.292	0.267	0.319	0.122

We have no information on the relative number of smallmouth bass inshore and offshore. We did observe seasonal changes in CPUE of smallmouth bass in our sampling near shore which may indicate onshore-offshore movement. CPUE in March and June averaged 2.8 fish per run. CPUE in April, July, and August averaged 1.6 fish per run.

DISCUSSION

Abundance

We estimated the combined abundance of northern squawfish, walleye, and smallmouth bass in John Day Reservoir at 135,000 fish. We felt the net result of biases we did not account for led us to a conservative estimate of the abundance of potential predators. Northern squawfish composed 76% of the potential predators in the reservoir. Underestimation of angler harvest because of failure to survey the entire reservoir, incomplete mixing of marked and unmarked fish, and underestimation of size-related differences in vulnerability all contributed to underestimation of northern squawfish.

The net effect on our estimate of smallmouth bass abundance of biases we did not account for is unknown but is probably not large. Our assumption of no mixing outside sampled areas probably led to an overestimation because some mixing did occur. The contribution of fish in the John Day River adjacent to our forebay sampling area also adds to the overestimation. Similarly our assumptions of no added mortality among marked fish and of recognition of all recaptures would have led to overestimation if in error. On the other hand, our assumption of equal vulnerability of all sizes to capture and a lack of angler harvest numbers from Rock Creek, Arlington, and Crow Butte would have caused underestimation.

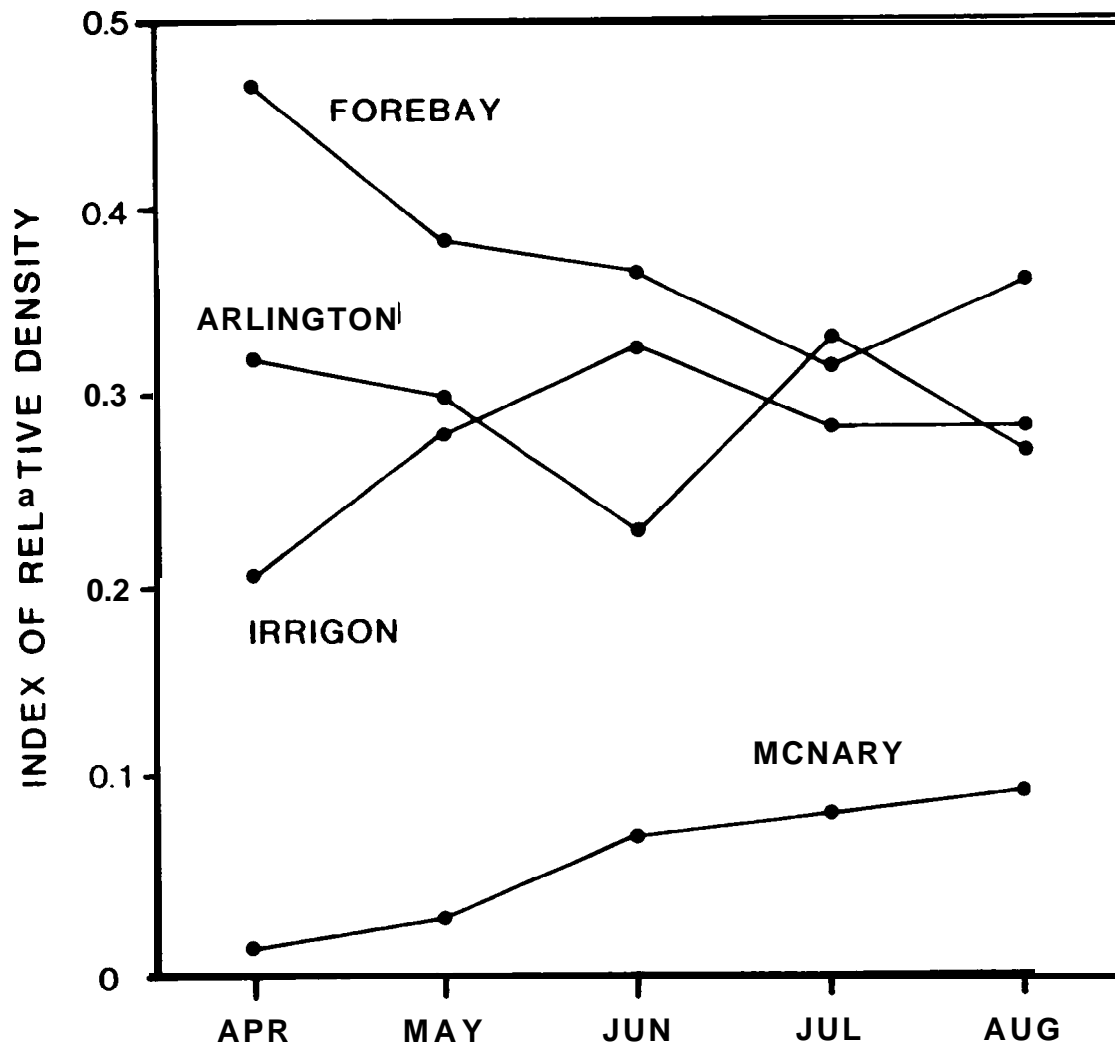


Figure 7. Index of relative density of smallmouth bass in four areas of John Day Reservoir, April-August. Index is based on catch per unit effort in three gears of fish with fork lengths greater than 250 mm 1984-86.

In the worst case our total estimate is within bounds of 60,000 and 50,000 based on the uncertainty associated with assumptions of the estimator and the precision related to sample sizes. Errors leading to overestimation were all on the order 50% or less. Of errors leading to underestimation of numbers, the assumption regarding mixing was most critical. This assumption resulted in a four-fold difference among northern squawfish and a twofold difference among smallmouth bass. All other assumptions leading to underestimation had effects of less than 50%. Estimates of precision were all of a magnitude of 100% or less. The combined multiplicative effect of all these uncertainties is approximately tenfold. However, many of these effects are in opposite directions and might cancel each other, and the likelihood of being wrong on all assumptions seems remote. In addition single mark and recapture estimates were not much larger than multiple mark and recapture estimates, implying that incomplete mixing, which caused most of the uncertainty, was not a problem. We therefore believe a "worst case" bound on our estimate is approximately fivefold.

Our estimates of predator density are all less than those reported by other authors. We estimate the density of northern squawfish in John Day Reservoir at 4.4 fish per hectare. The only other available estimate of northern squawfish density was 15 per hectare in Lake Washington (Bartoo 1977). We estimated walleye density at 0.8 per hectare. No density less than 7 fish per hectare is reported in a summary of the walleye literature by Colby et al. 1979. Similarly, we estimate density of smallmouth bass at 1.8 fish per hectare whereas Carlander (1977) reports no density less than 16 fish per hectare.

We believe low productivity in the reservoir, limited habitat and year-class failures, rather than underestimation, accounted for the lower densities of northern squawfish, walleye, and smallmouth bass than are reported in the literature. Low productivity would be expected to reduce standing crops of all predators. Primary production in the John Day Reservoir is probably limited by low retention of water, lack of nutrients, lack of littoral area, and fluctuations in water level related to hydropower operations.

Habitat for walleye and smallmouth bass is apparently limited as both were restricted to portions of the reservoir. Walleye were seldom found outside the upper reservoir. Smallmouth bass were most abundant in embayments that accounted for a small fraction of the reservoir. Density near literature values was approached in those preferred habitats.

Variable spawning success also appeared to contribute to the low number of walleye and northern squawfish. During our study, reproduction by walleye was below average and the population was composed primarily of fish from the large 1979 year class (Connally and Rieman 1988). Low recruitment of northern squawfish from 1975 through 1980 (Rieman and Beamesderfer 1988) may also have depressed the size of that population.

The numbers of predators in John Day reservoir was not constant from year to year. Our ability to discern these differences was limited by the precision of our estimates, but we did see a significant increase in northern squawfish estimates from 1984 to 1986. We expected to see annual variation

among all three predator populations because of variable spawning success (Connolly and Rieman 1988; Rieman and Beamesderfer 1988). An upward trend in recruitment in recent years may explain the 15%-20% annual increases in the number of northern squawfish. We also believe that the walleye population declined during the course of our study as fish from the 1979 cohort died and were not replaced by new recruits. A decline is implied by angler catch rate, which dropped from 17 hours per fish in 1983 to 50 hours per fish in 1984 and 64 hours per fish in 1985 and 1986 (Olson et al. 1988). However, this suspected decline was not reflected in our estimates of abundance.

Distribution

Uneven distribution of predators is probably related to the availability of prey and of habitat. We believe northern squawfish concentrated in the BRZ to take advantage of local concentrations or greater vulnerability of prey, including salmonids. Northern squawfish prefer low velocity microhabitats (Beamesderfer 1983; Faler et al. 1988) and feed by sight during daylight (Steigenberger and Larkin 1974). Predation may be minimized if salmonids migrate in fast-flowing water offshore, near the surface, at night, during periods of high flow and turbidity (Brown and Myle 1981). Dams may delay and concentrate migrants and provide low velocity refuges near areas of concentration for northern squawfish. Salmonids are not major prey items of northern squawfish in rivers under natural conditions (Brown and Myle 1981; Buchanan et al. 1981, Falter 1969). Northern squawfish are opportunistic predators (Brown and Myle 1981) and have been observed to feed heavily on salmonids at sites of release from hatcheries (Thompson 1959). Other work indicates that concentrations have consistently been associated with other dams in the system (Sims 1979; Uremovich et al. 1980).

Walleye were largely restricted to the upper reservoir. Walleye prefer shallow to moderate depths (15 m or less) and extensive littoral areas (Colby et al. 1979; McMahon et al. 1984). This type of habitat was most abundant in the upper reservoir. Depths averaged 10 m or less in the upper reservoir and embayments, and islands provided large littoral areas. Depths in the lower reservoir averaged 20-50 m, shorelines were steep with little littoral zone, and embayments and islands were rare.

Smallmouth bass density was greatest in forebay and Irrigon areas. Smallmouth bass prefer velocities less than 0.5 fps (Edwards et al. 1983). In Columbia and Snake river reservoirs, smallmouth bass are most abundant in protected embayments (Hjort et al. 1981; Palmer 1982). We also observed concentrations wherever embayments provided standing water habitat. Few embayments exist in McNary tailrace, which explains the low relative abundance of smallmouth bass there. Abundance was higher in the Irrigon area which included a very large embayment near Paterson, Washington. Embayments were smaller and less common in Arlington than in Irrigon, which is consistent with the lesser numbers in Arlington based on mark-recapture estimates. The large number in John Day forebay apparently resulted from the proximity of the John Day River. John Day Dam backs water into the lower 15 km of the John Day River, creating a slackwater that supports a large number of smallmouth bass. Recaptures of marked fish indicate that smallmouth bass range freely between the John Day River slackwater and the forebay.

Reasons for differences in distribution with size were species-specific. Relative density of northern squawfish in the BRZ increased with size. We suspect this size difference in distribution was related to size differences in food habits. Fish larger than 400 mm were much more piscivorous than smaller fish (Poe et al. 1988), hence they could capitalize on concentrations of vulnerable prey fish near the dam. Vigg et al. (1988) speculate that larger fish are also more able to maintain positions in areas of swift current prevalent in the BRZ.

The proportion of small walleye in McNary tailrace was greater than the proportion of large walleye found there. This difference may have been related to sex differences in spawning behavior, maturation, and longevity. Males spend more time on spawning areas and mature at smaller sizes than females (Colby et al. 1979). Females grow faster and live longer than males. We sampled a large number of ripe males in the 250-500 mm size range in McNary tailrace in March and April. The distribution of fish in the 250-500 mm size range may reflect these concentrations of males in spawning areas. The distribution of fish greater than 500 mm may reflect the shorter duration females spend in spawning sites.

Relative density of smallmouth bass was greater for smaller fish than for large fish in the forebay. The abundance of small fish in the forebay probably reflects the large area of favorable habitat provided by the John Day River slackwater. High exploitation by anglers could explain why a relatively large number of smallmouth bass larger than 250 mm was not also seen in the forebay. Exploitation in the lower reservoir averaged 0.45-0.94 as compared with 0.24-0.26 in the upper reservoir (Beamesderfer et al. 1987).

Seasonal movements by predators might be related to spawning and feeding. Northern squawfish typically overwinter in deeper, offshore areas of lakes (Olney 1975) or deeper, downstream portions of rivers (Hill 1962). Northern squawfish often migrate into or up rivers to spawn from May through July (Beamesderfer 1983) then disperse to summer feeding areas (Reid 1971; Olney 1975). Increased density in McNary tailrace in May and June may result from movement of spawners out of lower and midreservoir overwintering areas and into the upper reservoir to spawn. Hjort et al. (1981) suggest northern squawfish rely on free-flowing habitat in the upper reservoir to spawn. Peak density of northern squawfish in the BRZ in August may result from an influx of post-spawning fish. Up-reservoir movement for spawning may thus contribute to predation in the BRZ by placing a large number of predators nearby at the start of summer when warm temperature maximizes individual consumption.

Walleye appeared to migrate into McNary tailrace in March and April to spawn. After spawning they appeared to disperse into summer feeding areas down-reservoir. Colby et al. (1979) reported that walleye migrate from their overwintering grounds to their spawning grounds in spring and continue to their summer feeding grounds after spawning. Upstream movements into spawning areas are common and frequently occur into areas below impassable dams (Scott and Crossman 1973).

We saw few differences in patterns of distribution from year to year. The most obvious was in walleye where density in McNary tailrace was lower in 1985 than in 1984 or 1986. Walleye prefer temperatures of 3°-11°C for spawning, and time of spawning may vary seasonally depending on when suitable

temperature is reached (Colby et al. 1979). We surmise spawning ended earlier in 1985 and many spawners had already dispersed down reservoir prior to our sampling. We also saw some annual differences among smallmouth bass but as with month differences in relative abundance, we suspect this variation resulted from area differences in population dynamics rather than a redistribution of smallmouth bass from year to year. Connally and Rieman (1988) reported differences in year class strength and growth between smallmouth bass in the lower (Forebay and Arlington) and upper reservoir (Irrigon and McNary).

The inshore preferences of northern squawfish and walleye may have been related to increased availability of food in the littoral area and a preference for low velocity microhabitats. Current velocities of 1 fps or less are preferred by northern squawfish (Beamesderfer 1983). Water velocity probably exceeded 1 fps offshore throughout the reservoir during high flow from March through June. Mixing of surface water into the aphotic zone may have reduced offshore productivity and available prey. The seasonal decline in occurrence inshore may have been related to declining flow and current velocity offshore. Velocity may have approached that preferred by northern squawfish and offshore production and available prey may have increased as the reservoir became less riverine.

We observed increased CPUE of smallmouth bass in May and June. We suspect that changes resulted from movement onshore in May and June to spawn then back into deeper areas, which cannot be sampled, in July and August. The observed lack of movement between areas implies that a changing catch rate is not a result of up and down reservoir movements. Similar patterns of movement have been reported in numerous other populations of smallmouth bass (Scott and Crossman 1973; Montgomery et al. 1980).

The inshore distribution of northern squawfish, walleye, and smallmouth bass during at least part of the year implies our sampling was representative despite limited sampling offshore. We had little success sampling offshore because of current, barge traffic, and a snag-strewn bottom, but the majority of the northern squawfish and walleye populations appeared to occur inshore and were vulnerable to our gear. A majority of sexually mature smallmouth bass, which were also likely to spawn in inshore areas, were vulnerable to our sampling.

Potential Predation

Based on their number and distribution, northern squawfish appear to pose the greatest threat to migrating salmonids. Northern squawfish were the most abundant predator in John Day Reservoir, with an estimated number more than twice that of smallmouth bass or walleye. Northern squawfish were also the only predator to take advantage of the hypothesized greater vulnerability of salmonids below McNary Dam by congregating there. Based on number alone, smallmouth bass would be a greater threat than walleye, but this difference may be reduced by differences in distribution. A portion of the smallmouth bass population occurs in the John Day River arm slackwater where salmonids moving down the main channel would not be available. In addition, the number of walleye during the course of our study may have been misleading. We

believe the walleye population was depressed because of poor recruitment since 1979. One or a series of big year classes of walleye might drastically alter numbers and potential for predation.

We would expect some annual variation in losses with fluctuations in the number of predators driven by variable year-class strengths (Connally and Rieman 1988; Rieman and Beamesderfer 1988) and annual differences in predator distribution. We saw some evidence of annual variation in numbers of northern squawfish but uncertainties in estimates of abundance make annual variation difficult to detect. The magnitude of potential variation in loss to predation between years could be better addressed with simulations of predator populations regulated by variable recruitment. These simulations should also consider variations in distribution.

The uneven distribution of predators throughout the reservoir suggests predation is not evenly distributed throughout the reservoir. Estimates of predation need to be stratified by area to account for this uneven distribution. In addition, reservoir size may not be as critical as the nature of a reservoir in determining the magnitude of losses to predation. A small system with prime habitat might be equivalent to a large reservoir with poor habitat.

Seasonal changes in loss may be expected as predator distributions vary. Predation may increase as predators move into areas of increased salmonid vulnerability or abundance. An increase in predation may be expected as northern squawfish move into the BRZ in July and August. An increase might also be expected as predators move offshore in summer. All three predator species exhibited some increased use of offshore areas after June. Salmonids apparently migrate offshore (D. Dauble, Battelle Northwest Laboratory, personal communication) hence encounters between predators and prey would be reduced in spring when predators occur in inshore areas. In summer, when predators move offshore, offshore areas may no longer be the predation-free avenues of outmigration they were in the spring.

Estimating abundance and distribution of fish in a large reservoir is a difficult task subject to uncertainty in inferences from a sample of the population, uncertainty in assumptions of the estimators and noise from seasonal and annual variation in the system. No single approach or estimate is entirely satisfactory, but a series of alternatives may bound the range of uncertainty. Thus we cannot make point estimates with high confidence, but we can satisfy ourselves that abundance is within a limited range. Our results remain useful for estimating predation on salmonid smolts but dictate which questions can be answered. We cannot use our estimates of abundance and distribution to make estimates of predation suitable for partitioning unexplained smolt mortality between predation and other sources. We can, however, isolate predation and answer the question "do predators cause significant mortality of salmonid smolts in John Day Reservoir."

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REFERENCES

- Bartoo, N.W. 1977. Population parameter estimates and energy budgets for peamouth, northern squawfish and yellow perch in Lake Washington. Doctoral dissertation. University of Washington, Seattle.
- Beamesderfer, R.C. 1983. Reproductive biology, early life history, and microhabitat of northern squawfish (*Ptychocheilus oregonensis*) in the St. Joe River, Idaho. Master's thesis. University of Idaho, Moscow.
- Beamesderfer, R.C., and B.E. Rieman. In press. Size selectivity and bias in estimates of population statistics of smallmouth bass, walleye, and northern squawfish in a Columbia River Reservoir. North American Journal of Fisheries Management.
- Beamesderfer, R.C., B.E. Rieman, J.C. Elliott, A.A. Nigro, and O.L. Ward. 1987. Distribution, abundance, and population dynamics of northern squawfish, walleye, smallmouth bass, and channel catfish in John Day Reservoir, 1986. Report to Bonneville Power Administration (Contract DE-AI79-82BP35097), Portland, Oregon.
- Brown, L.R., and P.B. Moyle. 1981. The impact of squawfish on salmonid populations: A review. North American Journal of Fisheries Management. 1:104-111.
- Buchanan, D.V., R.M. Hooton, and J.R. Moring. 1981. Northern squawfish (*Ptychocheilus oregonensis*) predation on juvenile salmonids in sections of the Willamette River basin, Oregon. Canadian Journal of Fisheries and Aquatic Science 38:360-364.
- Carlander, K.D. 1977. Handbook of freshwater fishery biology, volume 2. Iowa State University Press, Ames.
- Chapman, D.G., and W.S. Overton. 1966. Estimating and testing between population levels by the Schnabel estimation method. Journal of Wildlife Management 30:173-180.
- Colby, P.J., R.E. McNicol, and R.A. Ryder. 1979. Synopsis of biological data for walleye, *Stizostedion v. vitreum* (Mitchell 1818). Food and Agriculture Organization of the United Nations Fisheries Synopsis Number 119.
- Connolly, P.J., and B.E. Rieman. 1988. Population dynamics of walleye and smallmouth bass and potential predation on juvenile salmonids in a mainstem Columbia River reservoir. In T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final report (Contract DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Ebener, M.P., and F.A. Copes. 1985. Population statistics, yield estimates, and management considerations for two lake whitefish stocks in Lake Michigan. North American Journal of Fisheries Management 5:435-448.

- Edwards, E.A., G. Gebhart, and O.E. Maughan. 1983. Habitat suitability information: Smallmouth bass. U.S. Fish and Wildlife Service, FWS/OBS-82/1 10.36, Washington, D.C.
- Elliott, J.M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates, 2nd edition. Freshwater Biological Association Scientific Publication 25, Ambleside, England.
- Everhart, W.H., A.W. Eipper, and W.D. Youngs. 1975. Principles of fishery science. Cornell University Press, Ithaca, New York.
- Faler, M.P., L.M. Miller, and K.I. Welke. 1988. Effects of variation in flow on distributions of northern squawfish in the Columbia River below McNary Dam. North American Journal of Fisheries Management 8: 30-35.
- Falter, C.M. 1969. Digestive rates and daily rations of northern squawfish in the St. Joe River, Idaho. Doctoral dissertation. University of Idaho, Moscow.
- Hill, C.W. 1962. Observations on the life histories of the peamouth (*Mylocheilus caurinus*) and the northern squawfish (*Ptychocheilus oregonensis*) in Montana. Proceedings of the Montana Academy of Sciences 72: 2227-2231.
- Hjort, R.C., B.C. Mundy, and P.L. Hulett. 1981. Habitat requirements for resident fishes in the reservoirs of the lower Columbia River. Report (Contract DACW57-79-C-0067) to U.S. Army Corps of Engineers, Portland, Oregon.
- King, T.A., J.C. Williams, W.D. Davies, and W.L. Shelton. 1981. Fixed versus random sampling of fishes in a large reservoir. Transactions of the American Fisheries Society 110: 563-568.
- McMahon, T.E., J.W. Terrell, and P.C. Nelson. 1984. Habitat suitability information: Walleye. U.S. Fish and Wildlife Service FWS/OBS-82/10.56, Washington, D.C.
- Montgomery, J.C., D.H. Fickeisen, and C.D. Becker. 1980. Factors influencing smallmouth bass production in the Hanford area, Columbia River. Northwest Science 54: 296-305.
- Mytle, J.B., and R. Lound. 1960. Confidence limits associated with means and medians of series of net catches. Transactions of the American Fisheries Society 89: 53-58.
- Millan, J.W. 1980. Fish predation on salmonid smolts in the Columbia River system in relation to the endangered species act. U.S. Fish and Wildlife Service Fisheries Assistance Office, unpublished report, Leavenworth, Washington.

- Neter, J., W Wasserman, and M.H. Kutner. 1985. Applied linear statistical models, second edition. Richard O. Irwin, Inc., Homewood, Illinois.
- Neves, R.J., S.L. Brayton, and L.A. Helfrich. 1985. Abundance and production of rainbow trout in the South Fork Holston River, Virginia. North American Journal of Fisheries Management 5:584-589.
- Nigro₁, A.A., R.C. Beamesderfer, J.C. Elliott, M.P. Faler, L.M. Miller, and B.L. Uremovich. 1985. Abundance and distribution of walleye, northern squawfish and smallmouth bass in John Day Reservoir, 1985. Report (Contract DE-AI79-82B535097) to Bonneville Power Administration, Portland, Oregon.
- Nigro₂, A.A., C.F. Willis, R.C. Beamesderfer, J.C. Elliott, and B.L. Uremovich. 1985. Abundance and distribution of walleye, northern squawfish, and smallmouth bass in John Day Reservoir and tailrace, 1983. Report (Contract DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Olney, F.E. 1975. Life history of the northern squawfish, *Ptychocheilus oregonensis* (Richardson), in Lake Washington. Master's thesis. University of Washington, Seattle.
- Olson, D.E., J.C. Elliott, and R.C. Beamesderfer. 1988. Status of the sport fishery sturgeon, walleye, smallmouth bass and other species in John Day Reservoir, 1983-86. In preparation.
- Overton, W.S.. 1965. A modification of the Schnabel estimator to account for removal of animals from the population. Journal of Wildlife Management 29:392-395.
- Palmer, D.E. 1982. Abundance, survival, distribution, and movements of selected fishes in Lower Snake River Reservoirs. Master's thesis. University of Idaho, Moscow.
- Poe, T.P., H.C. Hansel, S. Vigg, D.E. Palmer, and L.A. Prendergast. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River Reservoir: Part I. Feeding ecology of northern squawfish, walleye, smallmouth bass, and channel catfish during the juvenile salmonid smolt out-migration. In T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final report (Contract DE-AI79-82BP34796) to Bonneville Power Administration, Portland, Oregon.
- Raymond, H.L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. Transactions of the American Fisheries Society 108:505-529.
- Raymond, H.L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River basin. North American Journal of Fisheries Management 8:1-24.

- Reid, G.E. 1971. Life history of the northern squawfish *Ptychocheilus oregonensis* (Richardson), in the St. Joe River,, Idaho. Master's thesis. University of Idaho, Mscow.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.
- Rieman, B.E. 1987. Fishing and population dynamics of largemouth bass (*Micropterus salmoides*) in select northern Idaho lakes. Doctoral dissertation. University of Idaho, Mscow.
- Rieman, B.E., and R.C. Beamesderfer. 1988. Population dynamics of northern squawfish and potential predation on juvenile salmonids in a mainstem Columbia River Reservoir. In T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Rieman, B.E., R.C. Beamesderfer, L.J. Bledsoe, and S. Vigg. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River Reservoir: Part IV. Total loss and mortality of juvenile salmonids to northern squawfish, walleye, and smallmouth bass. In T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Robson, D.S., and H.A. Regier. 1971. Estimation of population number and mortality rates. Pages 131-165 in W.E. Ricker, editor. Methods for assessment of fish production in fresh waters, 2nd edition. International Biological Programme Handbook Number 3. Blackwell Scientific Publications, Oxford.
- Scott, W.B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184.
- Seber, G.A.F. 1982. The estimation of animal abundance and related parameters, 2nd edition. MacMillan Publishing Company, Inc., New York.
- Sims, C.W. 1979. Effects of dam operations and flow regulation on juvenile salmon and steelhead migrations in the Snake and Columbia rivers, 1973-1978. National Marine Fisheries Service, Research Summary Report, Seattle, Washington.
- Sims, C.W. and Ossiander. 1981. Migrations of juvenile chinook salmon and steelhead trout in the Snake River from 1973 to 1979. Report (Contract DACW68-78-C0038) to U.S. Army Corps of Engineers, Portland, Oregon.
- Slaney, P.A., and A.D. Martin. 1987. Accuracy of underwater census of trout populations in a large stream in British Columbia. North American Journal of Fisheries Management 7:117-122.

- Steel, R. G. D., and J. H. Torrie. 1980. Principles and procedures of statistics. McGraw-Hill, New York.**
- Steigenberger, L. W., and P. A. Larkin. 1974. Feeding activity and rates of digestion of northern squawfish (*Ptychocheilus oregonensis*). Journal of the Fisheries Research Board of Canada 31(4):411-420.**
- Thompson, R. B. 1959. Food of the squawfish *Ptychocheilus oregonensis* (Richardson) of the lower Columbia River. U.S. Fish and Wildlife Service, Fishery Bulletin 158:43-58.**
- Uremovich, B. L., S. P. Cramer, C. F. Willis, and C. O. Junge. 1980. Passage of juvenile salmonids through the ice-trash sluiceway and squawfish predation at Bonneville Dam 1980. Report (Contract DACW57-78-C0058) to U.S. Army Corps of Engineers, Portland, Oregon.**
- Vigg, S., H. C. Hansel, and T. P. Poe. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: Part II. Consumption rates, diel feeding chronology, and daily rations of northern squawfish, walleye, smallmouth bass, and channel catfish. In T. P. Poe and B. E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final report (Contracts DE-A179-82BP34796 and DE-A179-82BP35097) to Bonneville Power Administration, Portland, Oregon.**
- White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Report LA-8787-NERP, Los Alamos, New Mexico.**

Appendix Table 1. Statistical comparisons of catch per unit effort of northern squawfish among four areas of John Day Reservoir: Forebay, Arlington, Irrigon, and McNary. Comparisons are based on analyses of variance on transformed catch data and include three gear types.

Additional effects included, source of variation	df	F	P
None:			
Gear	2; 6, 178	459.6	<0.01
Area	3; 6, 178	21.1	<0.01
Gear and area	6; 6, 178	11.2	<0.01
Size:			
Gear	2; 1, 2356	535.6	<0.01
Area	3; 1, 2356	27.8	<0.01
Size	1; 1, 2356	295.6	<0.01
Gear and area	6; 1, 2356	16.5	<0.01
Gear and size	2; 1, 2356	93.6	<0.01
Area and size	3; 1, 2356	8.3	<0.01
Gear and area and size	6; 1, 2356	5.1	<0.01
Month:			
Gear	2; 6, 130	458.0	<0.01
Area	3; 6, 130	21.5	<0.01
Month	4; 6, 130	28.4	<0.01
Gear and area	6; 6, 130	10.6	<0.01
Gear and month	8; 6, 130	3.8	<0.01
Area and month	12; 6, 130	7.2	<0.01
Gear and area and month	24; 6, 130	4.9	<0.01
Year:			
Gear	2; 6, 154	475.3	<0.01
Area	3; 6, 154	21.0	<0.01
Year	2; 6, 154	40.0	<0.01
Gear and area	6; 6, 154	13.6	<0.01
Gear and year	4; 6, 154	11.4	<0.01
Area and year	6; 6, 154	7.8	<0.01
Gear and area and year	12; 6, 154	8.7	<0.01

Appendix Table 2. Statistical comparisons of catch per unit effort of northern squawfish between two areas of John Day Reservoir: boat-restricted zone and all other combined. Comparisons are based on analyses of variance on transformed electrofisher catch data.

Additional effects included, source of variation	df	F	P
None:			
Area	1; 2, 929	1, 351.2	<0.01
Size:			
Area	1; 5, 858	2.0	0.16
Size	1; 5, 858	1.0	0.31
Area and size	1; 5, 858	0.2	0.67
Mnth:			
Area	1; 2, 921	1,349.5	<0.01
Mnth	4; 2, 921	6.6	<0.01
Area and month	4; 2, 921	7.5	<0.01
Year:			
Area	1; 2, 925	1,114.4	<0.01
Year	2; 2, 925	8.4	<0.01
Area and year	2; 2, 925	11.6	<0.01

Appendix Table 3. Statistical comparisons of catch per unit effort of walleye among four areas of John Day Reservoir: Forebay, Arlington, Irrigon, and McNary. Comparisons are based on analyses of variance on transformed catch data and include three gear types.

Additional effects included, source of variation	df	F	P
None:			
Gear	2; 6,178	13.6	<0.01
Area	3; 6,178	186.6	<0.01
Gear and area	6; 6,178	6.2	<0.01
Size:			
Gear	2; 12,356	16.8	<0.01
Area	3; 12,356	198.3	<0.01
Size	1; 12,356	15.0	<0.01
Gear and area	6; 12,356	6.6	<0.01
Gear and size	2; 12,356	13.0	<0.01
Area and size	3; 12,356	26.1	<0.01
Gear and area and size	6; 12,356	14.2	<0.01
Month:			
Gear	2; 6,130	11.6	<0.01
Area	3; 6,130	192.6	<0.01
Month	4; 6,130	53.1	<0.01
Gear and area	6; 6,130	5.3	<0.01
Gear and month	8; 6,130	5.5	<0.01
Area and month	12; 6,130	25.3	<0.01
Gear and area and month	24; 6,130	3.2	<0.01
Year:			
Gear	2; 6,154	16.1	<0.01
Area	3; 6,154	193.5	<0.01
Year	2; 6,154	23.8	<0.01
Gear and area	6; 6,154	7.1	<0.01
Gear and year	4; 6,154	5.0	<0.01
Area and year	6; 6,154	8.9	<0.01
Gear and area and year	12; 6,154	4.6	<0.01

Appendix Table 4. Statistical comparisons of catch per unit effort of smallmouth bass among four areas of John Day Reservoir: Forebay, Arlington, Irrigon and McNary. Comparisons are based on analyses of variance on transformed electrofisher catch data.

Additional effects included, source of variation	df	F	P
None:			
Area	2; 2,770	79.2	<0.01
Size:			
Area	3; 5,540	97.4	<0.01
Size	1; 5,540	16.0	<0.01
Area and size	3; 5,540	9.2	<0.01
Mnth:			
Area	3; 2,754	76.8	<0.01
Mnth	4; 2,754	9.3	<0.01
Area and month	12; 2,754	1.4	0.17
Year:			
Area	3; 2,762	80.5	<0.01
Year	2; 2,762	18.4	<0.01
Area and year	6; 2,762	4.6	<0.01

Predation by Resident Fish on Juvenile Salmonids in a Mainstem
Columbia Reservoir: Part IV. Estimated Total Loss and Mortality
of Juvenile Salmonids to Northern Squawfish, Walleye,
and Smallmouth Bass

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Abstract - We estimated the loss of juvenile salmonids *Oncorhynchus* spp and steelhead *Salmo gairdneri* to predation by northern squawfish *Ptychocheilus oregonensis*, walleye *Stizostedion vitreum vitreum*, and smallmouth bass *Micropterus dolomieu*, in John Day Reservoir. Our estimates were based on daily prey consumption and predator numbers from 1983 to 1986. We estimated mortality based on estimates of the number of juveniles entering the reservoir during the April through August period of migration. The mean annual loss was 2.7 million juvenile salmonids. The 95% confidence interval estimated by Monte Carlo simulation ranged from 1.9 to 3.3 million fish. Northern squawfish accounted for 78% of the total loss. Walleye and smallmouth bass accounted for 13% and 9%, respectively. Twenty-one percent of the loss occurred in a small area immediately below McNary Dam at the head of the reservoir. We estimated that the three predator fishes consumed 14% of all juvenile salmonids that entered the reservoir with 95% confidence limits of 9% to 19%. Mortality changed by month and was higher late in the season. The range of monthly mortality estimates was 7% in June to 61% in August. Chinook salmon, which migrated in July and August experienced higher mortality from predation than other salmon and steelhead. Although we show uncertainties in the estimates, predation by resident fish predators in John Day Reservoir can easily account for previously unexplained mortality of juvenile salmonids. Alteration of the Columbia River by dams, and a decline in the number of salmonids could have increased mortality caused by predation, making predation more important than in the past.

Adult runs of anadromous salmon *Oncorhynchus* spp. and steelhead *Salmo gairdneri* in the Columbia River have declined dramatically from historic levels. Apparent survival of chinook salmon *O. tshawytscha* leaving the upper drainage as juvenile salmonids and returning as adults dropped from approximately 4% in 1964-68 to less than 0.8% in 1972 (Ebel 1977). Survival of steelhead declined similarly. The declines have been attributed primarily to development of the basin for hydroelectric power (Ebel 1977, Northwest Power Planning Council 1987a). At present as many as 9 run-of-the-river dams and reservoirs must be negotiated by juvenile salmonids emigrating from hatchery and natural production areas. Available estimates show that 10% to 45% of all juvenile salmonids that pass an individual dam and reservoir are lost (Sims and Osslander 1981; McKenzie et al. 1983; Sims et al. 1984, Fish Passage Center 1987). Some fish die from physical injury during passage of the dams (Schoeneman et al. 1961). Passage loss estimates represent only a portion of the total mortality, however, leaving a large part as unexplained. Substantial mortality occurs within the reservoirs (McKenzie et al. 1983; Northwest Power Planning Council 1986). Causes of reservoir mortality include nitrogen supersaturation, disease, and residualism (Ebel 1977; Raymond 1979; Leong and Barila 1983; Northwest Power Planning Council 1987b). Predation by resident fish has been suggested as a particularly important cause of mortality (Long et al. 1968; Raymond 1969). Existing data suggest that predation may be important in localized areas (Thompson 1959; Long et al. 1968; Uremovich et al. 1980; Bennett et al. 1983), but the evidence is circumstantial.

The objective of this paper is to estimate, with an appropriate confidence limit, the number of juvenile salmon and steelhead lost to resident fish predators in an entire Columbia River reservoir. We relate predation to approximations of the number of fish that enter the reservoir to estimate mortality and determine whether predation can account for the "unexplained" loss. We also compare predation mortality immediately below the dam with estimates of passage mortality at the dam to determine if many fish apparently lost to predators might actually have been killed at the dam.

The resident fish community in John Day Reservoir is complex and contains at least 30 identified species. Many of these fish may be piscivorous, but four species, northern squawfish *Ptychocheilus oregonensis*, walleye *Stizostedion vitreum vitreum*, smallmouth bass *Micropterus dolomieu*, and channel catfish *Ictalurus punctatus* are particularly effective predators on salmonids (Gray and Rondorf 1986; Poe et al. 1988). Studies on predator populations and prey consumption were restricted to these four species because of their apparent abundance and for reasons of cost and logistics. Complete data suitable for population estimates were available only for the first three species (Beamesderfer and Rieman 1988).

Study Area

John Day Reservoir is one of four "run-of-the-river" impoundments operated for hydroelectric power generation and navigation on the lower Columbia River between Oregon and Washington (Figure 1). It is formed by John Day Dam near Rufus, Oregon, and extends upstream 123 km to the base of McNary Dam near Umatilla, Oregon. The reservoir has a surface area of about 21,000 ha. Offshore depths range from about 10 m in the upper reservoir to 50 m in

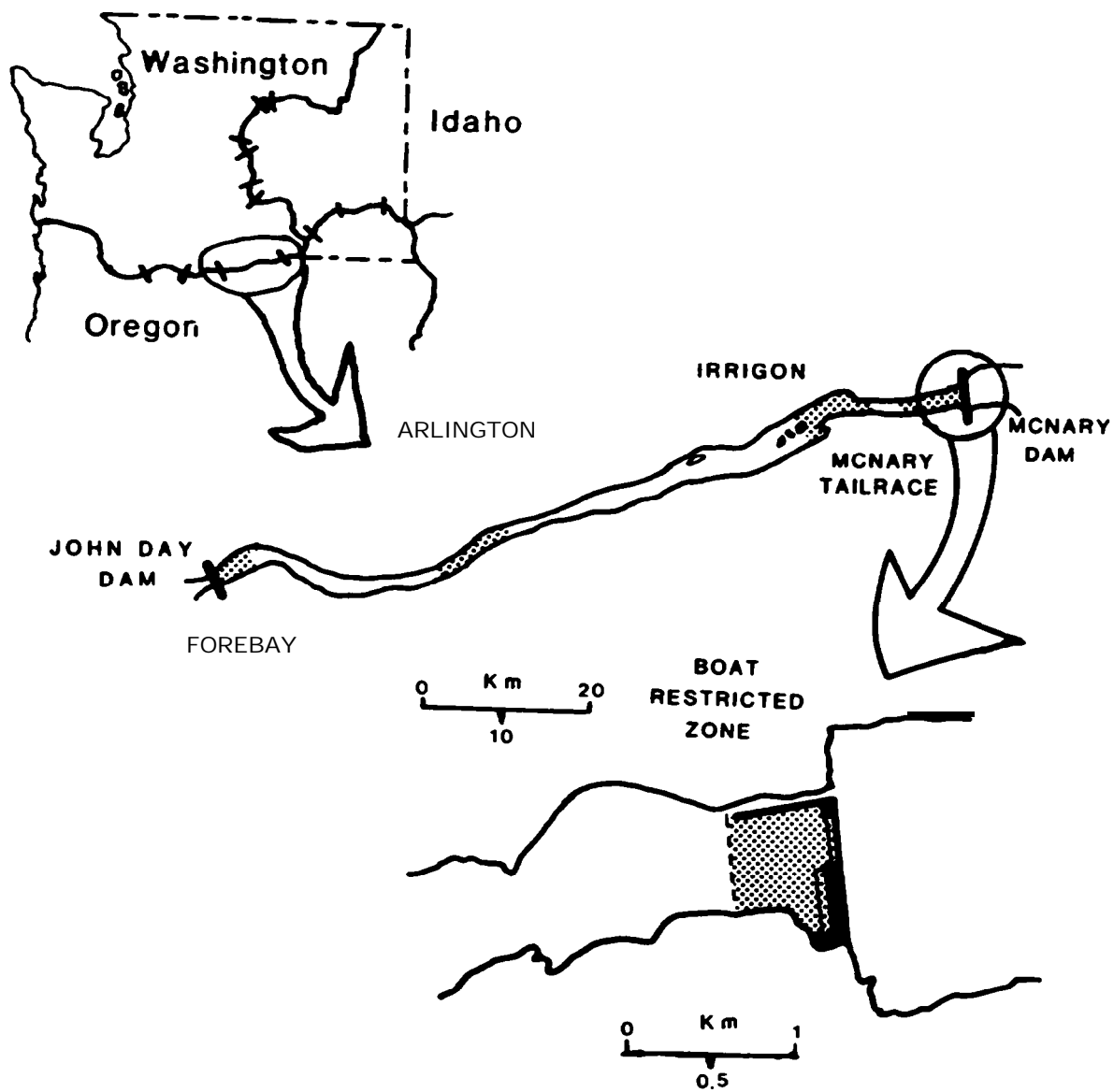


Figure 1. John Day Reservoir and the McNary Dam restricted zone (RZ) sampling area.

the forebay. The reservoir grades from a riverine to lentic character downstream through its length. Current is measurable throughout. Hydraulic residence time ranges from about 3 to 12 days (LaBolle 1984) and flow is regulated by McNary and John Day dams (Figure 1). The shoreline is typically steep, parent material is basalt, and littoral habitat is limited. Precipitation is low and shoreline vegetation is sparse. Water temperature ranges from 0° to 27°C with lows in January or February and highs in August. Juvenile salmon and steelhead are present in the reservoir year-round, but most fish migrate through the system as smolts from April through August. For a more detailed description of the study area readers are referred to Poe et al. (1988).

Methods

Predation Loss and Mortality

We estimated the mean monthly and total seasonal loss of juvenile salmonids to three predators, northern squawfish, walleye, and smallmouth bass, in John Day Reservoir for the period 1983 through 1986. We estimated the total loss by multiplying estimates of mean daily consumption (Vigg et al. 1988) and predator number (Beamesderfer and Rieman 1988) for each species of predator. We restricted the analysis to the April through August period because most salmonids migrate through the system at that time (Poe et al. 1988). We stratified estimates by month and, for northern squawfish, further stratified estimates by two sampling areas in the reservoir. We pooled data for northern squawfish from the McNary Dam boat-restricted zone (RZ), an area extending 700 m downstream from the face of the dam and separately pooled samples from all other sampling areas downstream (Figure 1). We pooled data by area because estimates of consumption by northern squawfish and density of northern squawfish near the dam were consistently and substantially higher than estimates in other areas (Beamesderfer and Rieman 1988; Vigg et al. 1988). We did not make estimates for walleye and smallmouth bass in the RZ. Those fish were not sampled in appreciable numbers in that area. We estimated the total loss of all salmonids and partitioned monthly estimates between salmon and steelhead to examine differences among stocks. We extrapolated estimates to a full month by multiplying daily consumption by the number of days in a month and to full season by summing estimates for each month. To represent each month, we pooled data for all years of study because sampling for consumption estimates was limited to only a portion of a month or was omitted in some months of individual years (Vigg et al. 1988). Our estimates represent predators larger than 250 mm fork length (northern squawfish and walleye) or 200 mm fork length (smallmouth bass) because consumption of juvenile salmonids was negligible by smaller predators (Vigg et al. 1988; Poe et al. 1988) and because recruitment to sampling gear limited population estimates to those sizes (Beamesderfer and Rieman 1988).

We estimated mean monthly and seasonal (April-August) mortality by dividing our loss estimates by the estimated numbers of salmon and steelhead passing the dam plus numbers released into the reservoir from hatcheries.

The loss estimates were calculated as

$$L_{hijk} = P_i R_{jk} C_{ijk} D_j G_{hij} \quad (1)$$

where L_{hijk} is the loss of salmonid h to predator i in month j and area k ; P_i is the number of predator species i in the reservoir; R_{jk} is the proportion of predators in area k , during month j (see equations 2 and 3); C_{ijk} is the daily consumption of all salmonids by predator i , in month j and reservoir area k ; D_j is the number of days in month j , and G_{hij} is the proportion of salmonid h in the diet of predator species i in month j . The reservoir area k applies only to northern squawfish. The proportion R_{jk} was estimated for each month based on relative catch-per-unit of sampling effort (CPUE) in each area weighted by the relative size of each area. The estimates were made as

$$R_{j1} = U_{j1} S_1 / (U_{j1} S_1 + U_{j2} S_2) \quad (2)$$

$$R_{j2} = 1 - (R_{j1}) \quad (3)$$

where U_{j1} or U_{j2} is the CPUE for squawfish in month j and area; $S_1=0.03$, the proportion of reservoir area contained within the RZ; and $S_2 = 0.97$, the proportion of reservoir area outside the RZ.

We made the mortality estimates as

$$A_{hj} = \sum_{ik} L_{hijk} / (m_{hj} + H_{hj}) \text{ and} \quad (4)$$

$$A = \sum_{hijk} L_{hijk} / (m_{hj} + H_{hj}) \quad (5)$$

where A_{hj} is the mortality of salmonid h in month j ; A is the total seasonal mortality of all salmonids; m_{hj} is the passage at McNary Dam for salmonid h in month j ; and H_{hj} is the number of hatchery produced salmonid h released in the reservoir during month j .

We approximated the standard deviation of the loss and mortality estimates by Monte Carlo simulation (Kirchner and Lauenroth 1987). We programmed our calculation as a Fortran algorithm that randomly selected values for each variable in the estimator from hypothetical distributions of each variable. We assumed normal distributions, described by the mean and variance of the mean from all observations or estimates of each variable. We ran 500 interactions of the program and calculated the mean and standard deviation for total and monthly estimates of loss and mortality. We described the 95% confidence limits for total loss and mortality as the range of estimates encompassing 95% of the simulations. Because we pooled data among years, our estimates represent the mean loss and mortality over the study and not a mean of individual years.

Estimates of prey consumption and composition - We estimated monthly mean consumption of all juvenile salmonids (juvenile salmonids consumed by an individual predator per day) based on stomach content and empirical models of evacuation rates. The consumption estimates are based on "Swenson's technique" (Swenson 1972; Swenson and Smith 1973). The method reconstructs an average diel feeding pattern from pooled stomach contents of a sample of

predators collected *in situ* by back-calculating the original weight, percent digestion, and time of ingestion of each prey fish. Consumption estimates are detailed in Vigg et al. (1988). The predator sampling design is detailed in Poe et al. (1988). Estimates were stratified by two reservoir areas and by months but pooled over years as described previously.

Because our consumption estimates were based on pooled stomach contents and consumption per predator, we were unable to calculate a variance directly. We used a second method based on consumption rates for individual predators to approximate a variance for the Swenson method estimates. For each predator in a given sample we estimated the number of salmonids consumed per day as

$$C = \sum_n 1/D90_n$$

where C is the number of salmonids consumed by a predator per day; $D90_n$ is the number of days to 90% digestion for the n th salmonid prey item. Ninety percent digestion was used as the criterion for turnover time since it represents the length of time a prey fish could be identified in the stomach contents, and because the digestion rate relation was assumed to change after 90% digestion is reached (the remainder is largely undigestible). Time for 90% digestion for each prey item was estimated from algorithms presented by Vigg et al. (1988). The estimators incorporate individual predator weight, temperature, and meal size as dependent variables. The meal size term was calculated from the sum of (1) the original weight of the specified salmonid prey & calculated from body or bone measurements (Vigg et al. 1988), (2) the original weights of any prey that were within 10% of the original weight and 20% of the percent digestion of the specified salmonid prey, and (3) the digested weight of all other food items in the stomach. We calculated the mean and variance of the mean consumption rate from all observations of individual predators. We assumed that the variance in our second method was representative of the variance in the consumption estimates from the Swenson technique. We approximated a variance of the monthly means for Swenson estimates (Appendix Table 1) by assuming an equal coefficient of variation between methods.

We estimated the relative proportions of each salmonid genus from the remains of all salmonids in stomach samples for each predator (Appendix Table 2). Salmonid remains were classified to genus based on bone morphology using methods detailed in Hansel et al. [in press] and the stomach analyses detailed in Poe et al. (1988). Variances for the proportions (P) were estimated as

$$vp = \frac{P(1-P)}{n}$$

where n equals the total number of salmonids identified in all stomachs (Zar 1984).

Estimates of predator number - We estimated the number of northern squawfish, the number of walleye larger than 250 mm and the number of smallmouth bass larger than 200 mm in the reservoir using mark-recapture data. Population estimates were made each year from 1984 to 1986 for northern squawfish and 1985 and 1986 for smallmouth bass using Over-ton's (1965) modification of the "Schnabel" estimator for marking and recovery within a

year. Recovery rates for walleye were low within the year of marking. We therefore made estimates for 1983 through 1986 using a "modified Petersen" method (Ricker 1975) based on marking in one year and recoveries in the in the following year. The walleye data were corrected for mortality in the year of tagging and for growth in both years of sampling. The population estimates and potential bias in estimates are detailed in Beamesderfer and Rieman (1988). We used the mean and the variance of the mean of available population estimates (Appendix Table 3) as the predator number in our loss estimator. We assumed those means to be representative of predator numbers for 1983 to 1986 even when estimates were limited to only 2 or 3 years in the 4-year period.

Estimates of northern squawfish catch rates - We used electrofishing samples collected at four locations in the reservoir to describe the catch rates (CPUE) of northern squawfish inside the RZ and throughout the remaining reservoir. Individual electrofishing runs of 900 seconds current-on time represented a sample. Sampling to describe the distribution of all predators is detailed in Beamesderfer and Rieman (1988). We stratified samples by month and pooled data over all years as with other variables, to calculate a mean and variance of the mean CPUE (Appendix Table 4).

Estimates of salmonid smolt numbers - We approximated the daily passage at McNary Dam for all juvenile salmon and steelhead from 1983 to 1986 after Giorgi and Sims (1987). The estimator relies on relationships of sampling efficiency and powerhouse flow derived only for yearling chinook salmon and steelhead. We assumed that the relationship for yearling chinook salmon was also representative of conditions for subyearling chinook salmon, coho salmon *O. kisutch*, and sockeye salmon *O. nerka*. To approximate the number of fish entering the reservoir and available to predators (Appendix Table 5), we subtracted numbers of fish removed at the collection facility (and subsequently transported downstream by barge or truck) and added the number of fish released into the reservoir from hatcheries. Daily estimates were summed over each month. The mean prey number and variance of the mean were calculated from the four yearly estimates in each month. We obtained all data on the number of salmonids collected at the dam and subsequently transported, on powerhouse flow, and on hatchery releases, from records of the Fish Passage Center of the Columbia Basin Fish and Wildlife Authority, Portland, Oregon.

Dam-Related Mortality

In our predation estimates we could not differentiate between healthy prey fish and moribund or dead fish killed in passage because we could not distinguish the condition of prey in gut samples. To consider the potential bias in our loss estimates, we estimated daily mortality attributed only to northern squawfish predation in the RZ sampling area. We then compared those estimates with estimates of mortality from dam passage on the same days. We assumed that a predation mortality estimate substantially larger than a dam mortality estimate was evidence that predators were taking live juvenile salmonids in addition to those lost during passage. We made daily predation loss and mortality estimates in the same fashion as described earlier. We did not, however, extrapolate beyond the days when sampling for consumption estimates was done. We projected daily mortality expected from passage at McNary Dam from 1984 through 1986, by weighting mortality for each passage

route. We used the assumptions of FISHPASS, a model developed by the U.S. Army Corps of Engineers (unpublished manuscript U.S. Army Corps of Engineers, Water Quality Section, Water Management Branch, Engineering Division, March 1986). Passage mortality was estimated as

$$U_1 = T_1 ((F m_1) + (1-F) m_2) + (1-T_1) m_3 \quad (6)$$

where U_1 is the expected mortality on day 1; T_1 is the proportion of total flow and fish passing through the turbines and turbine bypass; F is the proportion of salmonids successfully guided through the turbine bypass ($F = 0.75$ for steelhead and age 1 chinook salmon and $F = 0.40$ for all other salmon); $m_1 = 0.02$, the mortality fish passing through the turbine bypass; $m_2 = 0.15$, the mortality of fish passing through the turbines; and $m_3 = 0.02$, the mortality of fish passing over the spillway. We obtained data on daily flow and the proportion of flow through the turbines from records of the Fish Passage Center of the Columbia Basin Fish and Wildlife Authority, Portland, Oregon.

Results

Predation Loss and Mortality

We estimated a mean seasonal loss of 2.7 million (SD = 338,000) juvenile salmon and steelhead to fish predators in John Day Reservoir from 1983 through 1986. Our simulated 95% confidence interval was from 1.9 and 3.3 million.

Northern squawfish was the dominant predator in John Day Reservoir (Figure 2). Overall, northern squawfish accounted for 78% of the total salmonid loss; walleye and smallmouth bass accounted for 13% and 9%, respectively. Of the three predators, northern squawfish was the only one with an appreciable population in the McNary Dam RZ. We estimate that 26% of losses to northern squawfish and 21% of total losses (all predators; all areas) occurred in the RZ. Thus, most of the total salmonid loss to the three predators studied occurred in the main body of the reservoir. The relative importance of northern squawfish was highest in April and May (92% of total). Walleye and smallmouth bass increased in importance during July and August. Northern squawfish represented about 75% and 67% of the total loss in those months respectively (Figure 2).

The total estimated loss varied by month and was lowest in April and highest in July (Table 1). Peak losses in May and July (Table 1, Figure 2) coincided with peaks in salmonid numbers. Salmon were the most important (94%) salmonid consumed by predators in all months (Table 1) and the only genus found in predator stomachs during July and August. The loss of steelhead was highest in May (Table 1).

Our estimate of total loss was 14% of the number of salmon and steelhead that entered John Day Reservoir. The simulated confidence limits ranged from 9% to 19%. The estimated mortality rates were higher in July and August than earlier in the season (Table 1). Most of the difference was with mortality of

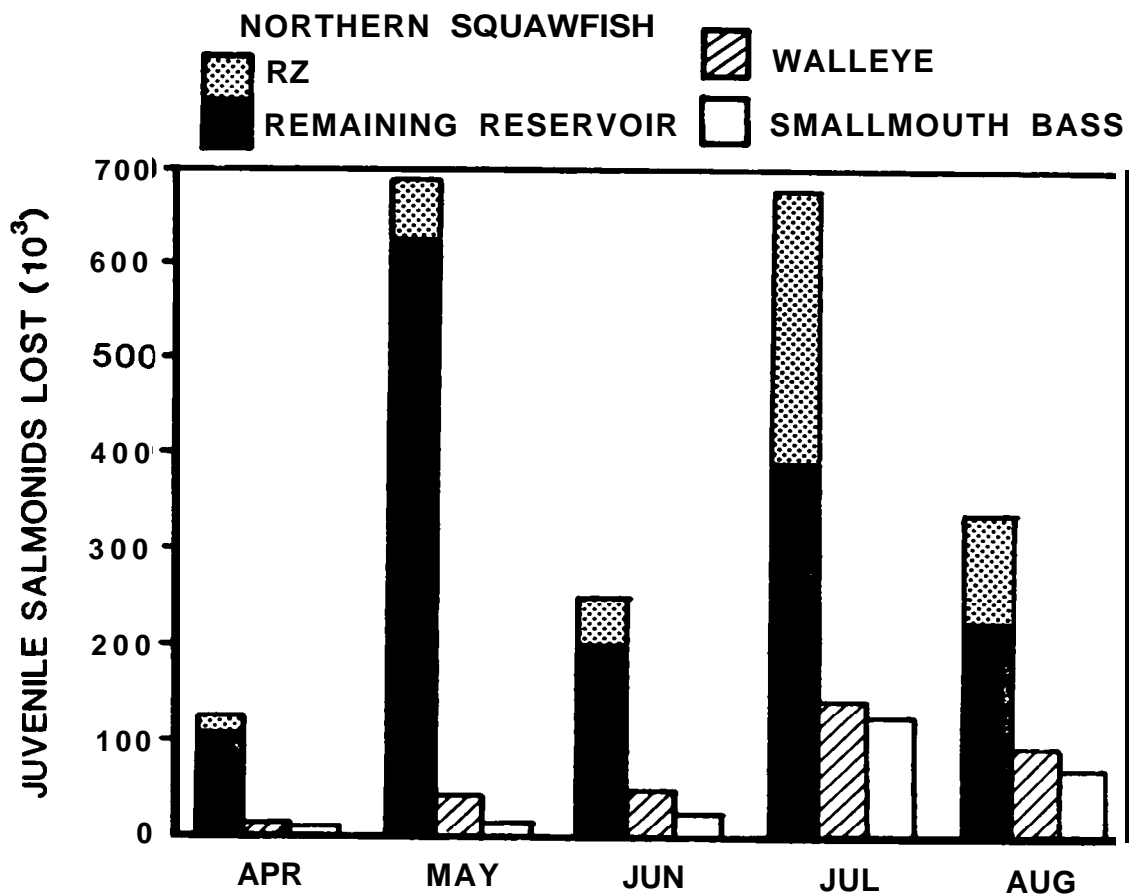


Figure 2. Estimated mean monthly number of juvenile salmonids lost to predation by northern squawfish, walleye, and smallmouth bass in John Day Reservoir from 1983 through 1986. Estimates for northern squawfish are stratified by the RZ sampling area (stippled) and the remaining reservoir (solid).

Table 1. Estimated loss and mortality from predation of juvenile salmonid and steelhead in John Day Reservoir by month 1983-1986.

Prey species, month	Number lost	SD	Mortality	SD
Salmon <i>Oncorhynchus</i> spp:				
April	118, 000	28, 000	0. 08	0. 034
May	633, 000	85, 300	0. 11	0. 017
June	297, 000	40, 200	0. 07	0. 025
July	968, 000	164, 200	0. 19	0. 062
August	468, 000	107, 900	0. 61	0. 298
Steelhead:				
April	15, 000	4, 900	0. 23	0. 061
May	107, 000	17, 100	0. 11	0. 031
June	26, 000	6, 300	0. 14	0. 089
July	(a)	(a)	(a)	(a)
August	(a)	(a)	(a)	(a)

a Estimates were not made for steelhead because numbers in the reservoir were *inconsequential*.

salmon. Estimated mortality of steelhead varied little from April to June. We did not estimate mortality for steelhead in July and August because numbers passing into the reservoir were inconsequential and because no steelhead were identified in predator stomachs.

Dam Related Mortality

Predicted mortality from passage at the dam was larger than, or of similar magnitude to, predation by northern squawfish immediately below the dam (RZ sampling area) from April through July. Passage mortality was less than half the estimated predation in August (Figure 3). Estimates of both mortalities increased from April to August (Figure 3).

Discussion

Our estimates support the hypothesis that predation accounts for the unexplained loss of juvenile salmonids in the Columbia River. Our estimates of 9% to 19% total mortality from predation in John Day Reservoir are obviously important relative to other known mortalities. Existing estimates of all mortality at individual projects (dam and reservoir) range from 10% to 45% (McKenzie et al. 1983; Sims and Ossiander 1981; Sims et al. 1984). Schoeneman et al. (1961) estimated that 2% of the fish passing over the spillway at a Columbia River dam and 11% of the fish passing through turbines were killed. Using present assumptions regarding passage, we approximated a combined spillway, turbine bypass and turbine mortality ranging from 4% to 10% at McNary Dam. Other causes for mortality are known in the Columbia River reservoirs. Ruggerone (1986) estimated that gulls consumed 2% of the salmon and steelhead passing Wanapum Dam. Loss to diseases also may be an important cause of mortality, particularly in hatchery fish (Leong and Barila 1983; Northwest Power Planning Council 1987a), but has never been quantified. Predation appeared to be at least equivalent to mortality at the dam and could easily represent the most important loss.

We believe predation is the major component of the unexplained mortality throughout the river. Because ours are the first estimates of predation in any Columbia River reservoir we cannot determine whether the magnitude of predation and numbers of predators are similar in other reservoirs or have changed in the river with time. Predators are common in other Columbia River reservoirs, however, and we know of no reason why densities should be substantially less than those in John Day. We believe it is reasonable to assume that they are not.

We also believe predation is more important than in the past, and has probably contributed to the decline of salmon and steelhead runs. The number of predator species has increased with introductions of exotics including walleye, smallmouth bass, and channel catfish. Dams have disrupted smolt migrations and undoubtedly stress and disorient juvenile salmonids making them more vulnerable to predators. Dams also delay smolt migrations, thereby increasing travel time through the reservoir (Raymond 1979). Juvenile salmonids are exposed to predation for longer periods and later in the season when consumption rates are high. Present smolt numbers are considerably lower

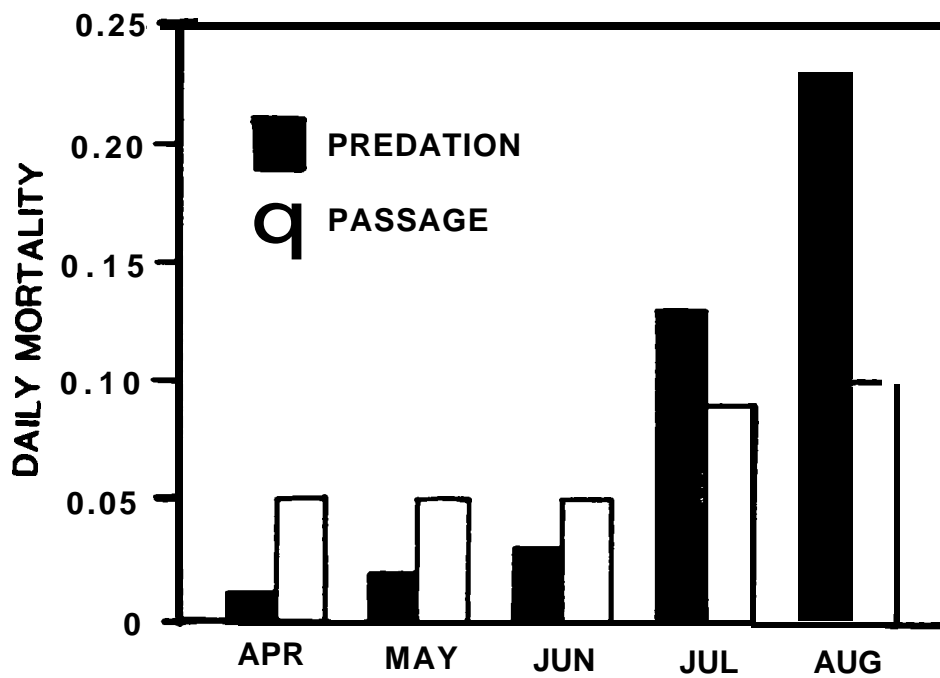


Figure 3. Estimated mortality of juvenile salmonids from predation immediately below McNary Dam and from injury during passage of McNary Dam. The data represent the means of daily estimates pooled by month, 1984-86.

than historic runs. Theory suggests that predators can also impose a compensatory mortality (Ricker 1950; Peterman 1977; Larkin 1979) and accelerate a decline started by some other stress (Coutant et al. 1979).

Northern squawfish were the major predator in our estimates and alone represented cause of substantial mortality on salmon and steelhead. Similar conclusions have been reached elsewhere, evidenced by the many attempts to control squawfish (*Ptychocheilus* spp.) populations (Brown and Moyle 1981). The universal importance of squawfish predation on salmonids is debated, however. Squawfish predation on salmonids has been documented in the Columbia River (Thompson 1959; Uremovich et al. 1980) and other systems (Foerster and Ricker 1941; Hartman and Burgner 1972; Steigenberger and Larkin 1974; Brown and Moyle 1981; Buchanan et al. 1981). Foerster and Ricker (1941) demonstrated that a reduction in northern squawfish predation increased production of sockeye salmon smolts in a lake. Others have concluded from food habit studies that squawfish predation in large rivers may be important only in unusual or artificial conditions. Unusual conditions might include localized hatchery releases or major habitat alterations (such as dams) that increase vulnerability or availability of salmonids as prey (Thompson 1959; Brown and Moyle 1981; Buchanan et al. 1981). We did find pronounced northern squawfish predation associated with McNary Dam. The estimated loss on a per mile basis immediately below the dam was more than 50 times that in the remaining reservoir. Predation outside the RZ, however, represented the largest part (79%) of the total loss. The average consumption of salmonids by individual northern squawfish away from the dam was relatively low (mean of 0.14 fish/day) (Vigg et al. 1988) and might, by the standards of other studies, be considered important. Obviously we must consider the predator population size. In a system supporting a population of 100,000 or more predators, even a low consumption rate can become important. Northern squawfish predation associated with the dam is not the only important predation in John Day Reservoir. Similar conclusions might be reached in other studies if the size of predator populations is considered.

The predation process can be dynamic and we believe that changes in the environment or characteristics of the prey can have an important influence on the loss (Peterman 1977; Coutant et al. 1979; Vigg 1988). We found, for example, that our loss and mortality estimates varied from month to month. We observed a nearly eight-fold variation in total loss and salmon mortality for all months. Vigg (1988) found that prey consumption by northern squawfish varied as a function of prey number and considered the relation to be indicative of a functional response (Peterman and Gatto 1978). The form of the relation may vary with season and in response to changes in the prey composition (Vigg 1988). Temperature also has an influence on predator metabolic demands and was related to maximum consumption rates for northern squawfish (Vigg and Burley 1988). Because of the variation in predation, mortality experienced by different stocks of salmonids migrating through the system will be different. Stocks of spring chinook salmon and steelhead that migrate primarily in April and May experience lower mortality from predation than fall chinook, which migrate primarily during the summer. Fall chinook salmon may also be more vulnerable to predators. Fall chinook salmon move more slowly through the reservoir (Miller and Sims 1984) and are smaller than spring chinook salmon or steelhead.

The dynamics of predation on salmonids should be an important consideration in Columbia River management. The timing of migration for salmon and steelhead will be influenced by hatchery release strategies and flow manipulations through the entire Columbia River hydropower system. The number and composition of prey can vary dramatically from year to year. Numbers can be increased through hatchery releases. Transportation programs designed to protect salmon and steelhead from any migration-related mortality by bypassing dams and reservoirs can reduce numbers in the lower reservoirs (Ebel 1977). Predator populations also vary. Predator abundance and population structure will vary with recruitment and the movement of strong and weak cohorts through all age classes. Sport fisheries and fishing regulations can influence predator population size and structure through exploitation. As a result we believe that as conditions change, the mortality from predation could differ substantially from that estimated here. Managers of salmon and steelhead stocks should consider that predator related mortality will vary both naturally and in response to manipulation of the system.

Our estimates made using several years of data incorporated some of the natural variation. Because of the necessity to pool data and the short duration of study, however, we could not partition sampling error and the inherent variation in our estimates. The source and magnitude of expected variation might be better detailed through dynamic simulation. Present studies provide additional data on the functional and physiological responses of predators, prey selection, and predator population dynamics. Simulations incorporating this information can provide a more detailed description of changes expected in predation. Description of changes in predation with normal variation, and manipulation of the reservoir environment, smolt abundance, and predator populations is addressed by Beamesderfer et al. (1988), Rieman and Beamesderfer (1988), and Connolly (1988).

Our estimates of salmon and steelhead lost to predation are substantial but we recognize important uncertainties. We cannot strictly partition all mortality into specific causes using available data. The causes probably are not independent. Predators are known to attack the most vulnerable or obvious prey (Coutant et al. 1979). Except for August, our estimates of predation immediately below the dam were less than, or similar to, our projections of the direct loss at the dam. We concluded that predators in the RZ are definitely taking live smolts late in the season. We cannot show, however, that they use live smolts exclusively during any period. Better information on the consumption of healthy and moribund prey below the dams will be necessary to precisely partition all components of mortality.

Our range of simulated estimates incorporates sampling error and seasonal variation, but does not account for the potential bias in each component of the estimator. Sampling in large systems such as John Day Reservoir is always difficult (Campbell 1979), and the probability of bias in population estimates may be particularly large. Beamesderfer and Rieman (1988) concluded that the potential bias in the population estimates used here could be several fold. The bias is probably negative, however, which means our estimates are probably conservative.

We do not account for loss to all predators, again making our estimates conservative. Channel catfish *Ictalurus punctatus* and white sturgeon *Acipenser transmontanus*, are both found in the reservoir, and are known to eat salmonids. White sturgeon probably use only moribund or injured juvenile salmonids, but channel catfish may eat healthy juvenile salmonids in important numbers (Bennett et al. 1983; Vigg et al. 1988). We do not have useful estimates of channel catfish numbers. The species is common in the reservoir (Beamesderfer and Rieman 1988), however, and could cause important mortality.

More reliable estimates of passage for subyearling chinook would be useful. Our estimates of mortality were dependent on estimates of salmonid passage numbers that are also subject to error of unknown magnitude. The passage estimator was based on relationships of sampling efficiency and powerhouse discharge developed for yearling chinook salmon and steelhead and for intermediate flow levels (Giorgi and Sims 1987). Because these fish and flows predominate during April and May, the method should provide "reasonably accurate" estimates of passage (and thus mortality) during that period (Giorgi and Sims 1987). Our extrapolation of passage estimates for other stocks and periods of higher powerhouse flow later in the year could be biased. Collection efficiency of subyearling chinook, which represented more than 80% of the salmonids passing the dam in late June, July and August may be lower than that assumed in the estimator. Estimates of collection efficiency for subyearling chinook are limited and highly variable but averaged approximately 30% during July and August 1986 (Swan and Norman 1987) compared with about 40% assumed in the passage estimator. An error of that magnitude would mean that our June through August estimates of salmon mortality are overestimated by 25%. The apparent increase in mortality in July and August, relative to earlier months, could be partly due to error in the passage estimator with changing salmonid stocks. Even with some bias in the estimates of passage, mortality of salmon late in the season would still be substantially higher than early.

We conclude that predation can be an important mortality of salmon and steelhead juvenile salmonids migrating through John Day Reservoir. Our estimates have limitations, but we believe they result in conservative estimates of loss and mortality. Predation can easily cause mortality equal to, or higher than, that caused by passage at the dams. Predation must be considered an important factor in management of depressed Columbia River stocks of salmon and steelhead if similar losses occur in other reservoirs.

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References

- Beamesderfer, R. C., and B. E. Rieman. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: Part III. Abundance and distribution of northern squawfish, walleye, and smallmouth bass. *In* T. P. Poe and B. E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report (Contracts DE-AI79-82BP34796 and DE-AI79-828BP35097) to Bonneville Power Administration, Portland, Oregon.
- Beamesderfer, R. C., B. E. Rieman, and S. Vigg. 1988. Simulation of predation by resident fish on juvenile salmonids in a Columbia River Reservoir. *In* T. P. Poe and B. E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report (Contracts DE-AI79-82BP34796 and DE-AI79-828BP35097) to Bonneville Power Administration, Portland, Oregon.
- Bennett, D. H., P. M. Bratovich, W. Knox, D. Palmer, and H. Hansel. 1983. Status of the warmwater fishery and the potential of improving warmwater fish habitat in the lower Snake reservoirs. Final Report (Contract DACW68-79-C0057) to U.S. Army Corps of Engineers, Portland, Oregon.
- Brown, L. R., and P. B. Moyle. 1981. The impact of squawfish on salmonid populations: A review. *North American Journal of Fisheries Management* 1: 104-111.
- Buchanan, D. V., R. M. Hooton, and J. R. Moring. 1981. Northern squawfish predation on juvenile salmonids in sections of the Willamette River Basin, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 360-364.
- Campbell, P. K. 1979. Predation principles in large rivers: A review. Pages 181-192 *in* H. C. Clepper, editor. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D. C.
- Connolly, P. J., and B. E. Rieman. 1988. Population dynamics of walleye and smallmouth bass and potential predation on juvenile salmonids in a mainstem Columbia River reservoir. *In* T. P. Poe and B. E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report (Contracts DE-AI79-82BP34796 and DE-AI79-828BP35097) to Bonneville Power Administration, Portland, Oregon.
- Coutant, C. C., R. B. Maben, and D. L. DeAngelis. 1979. Influences of physical and chemical alterations on predator-prey interactions. Pages 57-68 *in* H. C. Clepper, editor. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D. C.
- Ebel, W. 1977. Major passage problems. Pages 33-39 *in* E. Schwiebert, editor. Columbia River salmon and steelhead. American Fisheries Society Special Publication 10, Washington, D. C.

- Fish Passage Center. 1987. Smolt monitoring program annual report, Volume I: migrational characteristics and survival of Columbia Basin salmon and steelhead trout. Report (Contract DE-AI79-86BP61747 Project 86-30) to Bonneville Power Administration, Portland, Oregon.**
- Foerster, R.E., and W.E. Ricker. 1941. The effect of reduction of predacious fish on survival of young sockeye salmon at Cultus Lake. Journal of the Fisheries Research Board of Canada 5:315-336.**
- Giorgi, A.E., and C.W. Sims. 1987. Estimating the daily passage of juvenile salmonids at McNary Dam on the Columbia River. North American Journal of Fisheries Management 7:215-222.**
- Gray, G.A., and D.W. Rondorf. 1986. Predation on juvenile salmonids in Columbia Basin Reservoirs. Pages 178-185 In G.E. Hall and M.J. Van Den-Avyle, editors. Reservoir fisheries management: strategies for the 80's. Southern Division American Fisheries Society, Bethesda, Maryland.**
- Hansel, H.C., S.D. Duke, P.T. Lofy, and G.A. Gray. In press. Use of diagnostic bones to identify and estimate original lengths of ingested prey fish. North American Journal of Fisheries Management.**
- Hartman, W.L., and R.L. Burgner. 1972. Limnology and fish ecology of sockeye salmon nursery lakes of the world. Journal of the Fisheries Research Board of Canada 29:699-715.**
- Kirchner, T.B., and W.K. Lauenroth. 1987. Ecological modeling using microcomputers. Colorado State University, Natural Resource Ecology Laboratory and Range Science Department, Fort Collins.**
- La Bolle, L.D. 1984. Importance of the upper littoral zone as a rearing area for larval and juvenile fishes in a Columbia River impoundment. Master's thesis. Oregon State University, Corvallis.**
- Larkin, P.A. 1979. Predator-prey relations in fishes: an overview of the theory. Pages 13-20 in H.C. Clepper, editor. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D.C.**
- Leong, J.C., and T.Y. Barila, editors. 1983. Proceedings: Workshop on viral disease of salmonid fishes in the Columbia River Basin. Bonneville Power Administration Special Publication, Portland, Oregon.**
- Long, C.W., R.F. Krecma, and F.J. Ossiander. 1968. Research on fingerling mortality in Kaplan turbines-1968. U.S. Bureau of Commercial Fisheries, Progress Report, Seattle, Washington.**
- McKenzie, D., D. Weitkamp, T. Schadt, D. Carlile, and D. Chapman. 1983. 1982 systems mortality study. Battelle Pacific Northwest Laboratories, Report to Chelan County P.U.D. (Contract 2311 204052), Grant County P.U.D. (Contract 2311 204258), and Douglas County P.U.D. (Contract 2311 204080), Richland, Washington.**

- Miller, D.R., and C.W. Sims. 1984. Effects of flow on the migratory behavior and survival of juvenile fall and summer chinook salmon in the John Day Reservoir. Report (Contract DE-AI79-83BP39645) to Bonneville Power Administration, Portland, Oregon.
- Northwest Power Planning Council. 1986. Columbia River basin fishery planning model. Northwest Power Planning Council, Technical Discussion Paper, Portland, Oregon.
- Northwest Power Planning Council. 1987a. Columbia River Basin fish and wildlife program. Northwest Power Planning Council, Portland, Oregon.
- Northwest Power Planning Council. 1987b. Draft five year research plan by the fish disease technical work group, August 20, 1987. Northwest Power Planning Council, Portland, Oregon.
- Overton, W.S. 1965. A modification of the Schnabel estimator to account for removal of animals from the population. *Journal of Wildlife Management* 19:392-395.
- Poe, T.P., H.C. Hansel, S. Vigg, and L.A. Prendergast. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: Part I. Feeding ecology of northern squawfish, walleye, smallmouth bass, and channel catfish during the salmonid smolt out-migration. In T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to the Bonneville Power Administration, Portland, Oregon.
- Peterman, R.J. 1977. A simple mechanism that causes collapsing stability regions in exploited salmon populations. *Journal of the Fisheries Research Board of Canada* 34:1130-1142.
- Peterman, R.M., and M. Gatto. 1978. Estimation of functional responses of predators on juvenile salmon. *Journal of the Fisheries Research Board of Canada* 35:797-808.
- Raymond, H.L. 1969. Effect of John Day Reservoir on the migration rate of juvenile chinook salmon and steelhead in the Columbia River. *Transactions of the American Fisheries Society* 98:513-514.
- Raymond, H.L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966-1975. *Transactions of the American Fisheries Society* 108:505-529.
- Ricker, W.E. 1950. Cycle dominance among Fraser River sockeye. *Ecology* 31:6-26.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191.

- Rieman, B. E., and R. C. Beamesderfer. 1988. Population dynamics of northern squawfish and potential predation on juvenile salmonids in a Columbia River reservoir. In T. P. Poe and B. E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Ruggerone, G. T. 1986. Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam Transactions of the American Fisheries Society 115:736-742.
- Schoeneman, D. E., R. T. Pressey, and C. D. Junge. 1961. Mortalities of downstream migrant salmon at McNary Dam Transactions of the American Fisheries Society 90:58-72.
- Sims, C. W., A. E. Giorgi, R. C. Johnsen, and D. A. Brege. 1984. Migrational characteristics of juvenile salmon and steelhead in the Columbia River basin- 1983. Report (Contract DACW57-83-F-0314) to U.S. Army Corps of Engineers, Portland, Oregon.
- Sims, C. W., and F. J. Osslander. 1981. Migrations of juvenile chinook salmon and steelhead trout in the Snake River from 1973 to 1979. Report (Contract DACW68-78-C0038) to U.S. Army Corps of Engineers, Portland, Oregon.
- Steigenberger, L. W., and P. A. Larkin. 1974. Feeding activity and rates of digestion of northern squawfish (*Ptychocheilus oregonensis*). Journal of the Fisheries Research Board of Canada 31:411-420.
- Swan, G. A., and W. F. Norman. 1987. Research to improve subyearling chinook salmon fish guiding efficiency at McNary Dam 1986. Report (Contract DACW68-84-H-0034) to U.S. Army Corps of Engineers, Portland, Oregon.
- Swenson, W. A. 1972. Food competition between walleye, *Stizostedion vitreum vitreum* (Mitchill) and sager, *Stizostedion canadense* (Smith), in Lake of the Woods, Minnesota. Doctoral dissertation. University of Minnesota.
- Swenson, W. A., and L. L. Smith, Jr. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*). Journal of the Fisheries Research Board of Canada 30:1327-1336.
- Thompson, R. B. 1959. Food of the squawfish *Ptychocheilus oregonensis* (Richardson) of the lower Columbia River. U.S. Fish and Wildlife Service, Fisheries Bulletin 158:43-58.
- Uremovich, B. L., S. P. Cramer, C. F. Willis, and C. O. Junge. 1980. Passage of juvenile salmonids through the ice-trash sluiceway and squawfish predation at Bonneville Dam Report (Contract DACW57-78-C-0058) to U.S. Army Corps of Engineers, Portland, Oregon.

- Vigg, S. 1988. Functional response of northern squawfish predation to salmonid prey density in McNary tailrace, Columbia River. *In* T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Vigg, S., T.P. Poe, L.A. Prendergast, and H.C. Hansel. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: Part II. Consumption rate, diel feeding chronology, and daily rations of northern squawfish, walleye, smallmouth bass, and channel catfish. *In* T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Vigg, S., and C.C. Burley. 1988. Maximum consumption rates of northern squawfish in John Day Reservoir, Columbia River. *In* T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Zar, J.H. 1984. Biostatistical analysis, 2nd edition. Prentice-Hall, Englewood Cliffs, New Jersey.

Appendix Table 1. Estimated consumption rates of juvenile salmonids by predator fish in John Day Reservoir by month, 1983-86. Consumption rate = mean number of smolts eaten per day per individual predator. Data are from Vigg et al. 1988.

Predator species, area^a, month	Sample size	Consumption rate	Variance
Northern squawfish:			
Boat Restricted zone;			
April	242	0.14	2.3 x 10 ⁻⁴
May	424	0.49	11.4 x 10 ⁻⁴
June	614	0.36	14.3 x 10 ⁻⁴
July	589	2.03	102.6 x 10 ⁻⁴
August	208	0.40	25.2 x 10 ⁻⁴
Below Boat Restricted Zone;			
April	264	0.04	1.2 x 10 ⁻⁴
May	586	0.25	6.1 x 10 ⁻⁴
June	469	0.09	3.2 x 10 ⁻⁴
July	243	0.15	12.4 x 10 ⁻⁴
August	434	0.09	4.5 x 10 ⁻⁴
Walleye:			
April	231	0.02	0.9 x 10 ⁻⁴
May	284	0.11	10.2 x 10 ⁻⁴
June	297	0.12	11.4 x 10 ⁻⁴
July	70	0.41	197.4 x 10 ⁻⁴
August	77	0.21	83.9 x 10 ⁻⁴
Smallmouth bass:			
April	293	<0.01	0.1 x 10 ⁻⁴
May	673	0.01	0.3 x 10 ⁻⁴
June	793	0.02	0.5 x 10 ⁻⁴
July	608	0.12	2.2 x 10 ⁻⁴
Augu	489	0.07	7.2 x 10 ⁻⁴

^a Estimates for walleye and smallmouth bass do not include the boat restricted zone because very few fish were collected there.

Appendix Table 2. Estimated proportions of salmon *Oncorhynchus* spp. identified from all salmonids found in predator fish from John Day Reservoir by month, 1983-86. Data are from Poe et al. 1988.

Predator species, month	Sample size ^a	Proportion	Variance
Northern squawfish:			
April	131	0.88	9.0×10^{-4}
May	567	0.85	2.3×10^{-4}
June	272	0.91	2.9×10^{-4}
July	837	1.00	--b
August	132	1.00	--b
Walleye:			
April	12	1.00	--
May	45	0.91	18.5×10^{-4}
June	27	0.96	14.4×10^{-4}
July	3	1.00	--b
August	7	1.00	--b
Smallmouth bass:			
April	--	1.00	--
May	7	1.00	--
June	22	0.96	18.5×10^{-4}
July	28	1.00	--b
August	13	1.00	--b

^a Total prey identified as salmonids.

^b Variance assumed to be 0 because few steelhead were in the reservoir.

Appendix Table 3. Estimated number of predator fish present in John Day Reservoir. Estimate for northern squawfish is the mean from 1984-86. Estimate for walleye is the mean from 1983-86. Estimate for smallmouth bass is the mean from 1985-86. Data are from Beamesderfer and Rieman 1988.

Predator	Sample size	Number	Variance
Northern squawfish	3	85,000	96.4 x 10 ⁶
Walleye	4	12,500	2.1 x 10 ⁶
Smallmouth bass	2	34,000	9.0 x 10 ⁶

Appendix Table 4. Estimated catch rate (CPUE) for northern squawfish in two areas of John Day Reservoir by month, 1984-86. The unit of effort was 900 seconds of electrofishing current-on time. Data are from Beamesderfer and Rieman 1986.

Area Mnth	Sample size	CPUE	Variance
McNary Dam Boat			
Restricted Zone:			
April	33	6.03	1.562
May	26	8.81	4.880
June	31	10.81	4.753
July	35	8.63	2.130
August	32	9.94	2.921
Reservoir Below Boat			
Restricted Zone:			
April	498	0.35	0.002
May	586	0.54	0.003
June	635	0.51	0.004
July	554	0.43	0.003
August	501	0.28	0.009

Appendix Table 5. Estimated number of juvenile salmon and steelhead that entered John Day Reservoir by month, 1983-86. The estimates are the means of all four years.

Prey species, month	Number	Variance
Salmon <i>Oncorhynchus</i>^a spp:		
April	1, 567, 000	1. 37 x 10 ¹¹
May	5, 894, 000	1. 81 x 10 ¹¹
June	4, 465, 000	1. 33 x 10 ¹²
July	5, 246, 000	1. 28 x 10 ¹²
August	801, 000	1. 64 x 10 ¹¹
Steelhead:		
April	129, 000	1. 14 x 10 ⁹
May	955, 000	3. 94 x 10 ¹⁰
June	210, 000	4. 11 x 10 ⁹
July	3, 000	7. 56 x 10 ⁵
August	<1, 000	6. 00 x 10 ³

a Salmon include yearling chinook, subyearling chinook, coho ad sockeye. Yearling chinook represent about 80% all salmon in April and May. Subyearling chinook represent about 95% of all salmon in June, July, and August.

Population Dynamics of Northern Squawfish and Potential Predation
on Juvenile Salmonids in a Columbia River Reservoir

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Abstract

Northern squawfish *Ptychocheilus oregonensis* are an important predator on salmonid smolts in Columbia River reservoirs. To better understand predation we described growth, mortality, and the variation in year-class strength of northern squawfish in John Day Reservoir. We used a correlation analysis to examine variables related to recruitment. We used simulations to describe expected changes in predation caused by variation in recruitment or by exploitation. Growth of northern squawfish in John Day Reservoir was high relative to other populations. Estimates of mortality were uncertain but a best estimate of 0.25 (instantaneous annual) was equivalent to mortality estimated in a similar population and mortality estimated from an empirical model. Indexes of year-class strength varied, but recruitment was not obviously related to environmental variables. Year-class strength was negatively associated with concurrent year-class strength of walleye *Stizostedion vitreum vitreum* another predator. Simulated predation varied with recruitment and trends increasing or decreasing by more than 50% of the mean developed over periods of about 10 years. Simulated predation declined with exploitation. Sustained exploitation on the order of 10% to 20% annually reduced predation by 50% or more. The magnitude of change was related to reproductive compensation. We believe that limited, but sustained, exploitation of northern squawfish provides an alternative to more radical control measures. We are uncertain about the resilience of northern squawfish populations, however, and some risk exists that any exploitation could aggravate predation if exploitation is not sustained. Any control program should evaluate compensation in predators. Longterm studies probably will be necessary to distinguish changes in predation caused by predator removals from changes caused by inherent variation.

In the Columbia River basin, anadromous salmonids (*Oncorhynchus* spp., *Salmo gairdneri*) represent an important economic and social resource. Stocks declined in recent history. Major changes in survival of migrating juveniles are attributed to the development of hydroelectric power (Ebel 1977; Raymond 1988). Recent information indicates that a dominant part of the loss may occur within project reservoirs (Northwest Power Planning Council 1986). Predation by resident fishes has been considered an important part of the reservoir mortality (Ebel 1977; Raymond 1979). Rieman et al. (1988) estimated that three predators, northern squawfish *Ptychocheilus oregonensis*, walleye *Stizostedion vitreum vitreum* and smallmouth bass *Micropterus dolomieu* consumed 9% to 19% of all juvenile salmonids that entered the John Day Reservoir on an annual basis. Northern squawfish accounted for about 80% of the total loss.

Reduction in northern squawfish numbers could improve salmon and steelhead survival. Predation by northern squawfish was an important limitation on sockeye salmon *O. nerka* survival in Cultus Lake, British Columbia, where an eradication program produced a substantial increase in production (Foerster and Ricker 1941). Since then eradication programs targeting squawfish spp. have been widespread (Brown and Myle 1981). Similar programs have been considered for the Columbia River. Typical approaches to northern squawfish control have been radical and include the use of toxicants, explosives, or intensive trapping and netting (e.g. Jeppson 1957; Jeppson and Platts 1959; MacPhee 1969; Hamilton et al. 1970; Rulifson 1984). Although some successes have been reported, none of these programs appear to have been sustained by management. The reasons for not maintaining removal programs are unclear. However logistic, economic, and environmental constraints or a failure to obtain or recognize the desired result may make extensive eradication efforts difficult or unappealing. Problems could be compounded on large reservoirs. To remove the majority of northern squawfish from any single reservoir may prove difficult. To control predators over several or all reservoirs in the Columbia River system might be a monumental task.

The loss to predation must be a function of predator number and ultimately the production and dynamics of the predator populations. Large changes in number and production of fish stocks can result from minor changes in the processes of growth and mortality (Ricker 1963, 1975). Such changes are evident with exploitation of long lived, slow growing stocks (Ricker 1963; Adams 1980; Francis 1986). We hypothesize that limited exploitation of a predator population can result in important changes in population structure, production, food consumption, and ultimately, predation. Even if a major part of a predator population cannot be removed, significant reductions in predation can result from restructuring the population through limited but sustained exploitation.

Although growth and mortality can be important, reproduction is often considered the single most important process regulating individual fish stocks (LeCren 1960; Gulland 1978; Shepherd and Cushing 1980). If mean annual recruitment declines, the predator population can eventually decline by a similar magnitude. Environmental variables have commonly been tied to reproductive success. Flow or water level might be important with *Ptychocheilus* spp. (Myle et al. 1983; Haynes et al. 1984; La Bolle 1984).

Factors such as reservoir elevation have been used to control undesirable stocks (Everhart et al. 1975). Manipulation of the predator's environment could provide a means of limiting recruitment and an alternative means of limiting predation. Reproduction can also be stock related and resilient, and production might actually increase under exploitation (Ricker 1954; Goodyear 1980). Attempts to control a predator population might actually aggravate predation by increasing the recruitment and numbers of young, rapidly growing and feeding predators.

We know little about the population dynamics of northern squawfish. The intent of this paper is to document information on growth, mortality and reproductive success of northern squawfish in a Columbia River reservoir and to examine the potential influence of recruitment and exploitation on predation. Our objectives are (1) to describe the variation in predation expected from inherent variation in the population and (2) to determine whether alternatives for managing predation exist through manipulation of factors that influence predator recruitment, and through intensive or limited exploitation.

We used simulations to describe the potential changes in predation by northern squawfish given our best estimates of growth and mortality. We used a range of recruitment assumptions to bound our results and to describe a range of responses in predation that might result from both intensive and limited, but sustained predator removal.

Study Area

John Day Reservoir is one of four "run-of-the-river" impoundments operated for hydroelectric power generation and navigation on the lower Columbia River between Oregon and Washington. The reservoir is 123 km long with a surface area of about 21,000 ha. Offshore depths range from 10 m in the upper reservoir to 50 m near John Day Dam. The reservoir grades from a riverine to a lentic character through its length, but current is measurable throughout. Hydraulic residence time ranges from 3 to about 12 days (La Bolle 1984), and daily flow pattern is regulated through McNary Dam at the head of the reservoir and John Day Dam. The shoreline is typically steep, parent material is basalt, and littoral habitat is limited. Precipitation is low and shoreline vegetation is limited. Water temperature ranges from 0 to 27°C with lows in January or February and maximums in August. Juvenile salmon and steelhead are present in the reservoir year-round, but most of the fish migrate through the system as smolts from April through August.

Methods

We used 4 years of data and samples from a study of resident fish predators in John Day Reservoir (Beamesderfer et al. 1987) to estimate growth, mortality and variation in year class strength of northern squawfish. A total of 10,993 squawfish were sampled throughout the reservoir using a variety of gear. All fish collected during sampling were marked with individually identifiable "spaghetti" tags and a fin clip specific to year of capture. Lengths were taken on all fish in the sample, and scales were collected from a subsample. Detailed descriptions of the sampling program are in Nigro et al. (1985) and Beamesderfer et al. (1987). The length frequency, scale collection, and mark recovery data from these samples provided the basis for our population analysis.

We used a minimum of ten scales from every 25 mm length group for analysis in each sample year. Scale impressions were made in acetate strips and interpreted independently by two people using standard aging techniques as outlined by Jearld (1983).

We estimated age composition of the population from the length frequency of the total sample and an age-length key developed for each year. We corrected the length frequencies for differential gear vulnerability. We made corrections based on size related vulnerability described in a concurrent mark and recapture experiment (Beamesderfer and Rieman in press).

Growth and Mortality

Growth was estimated from a total sample of 893 scales. Measured distances from focus to individual annuli and to the scale margin were recorded during aging. Fork length at annulus formation was backcalculated as described by Bagenal and Tesch (1978). To describe growth for the purposes of our simulations, we fit the estimated mean length-at-age with the von Bertalanffy model (Ricker 1975). Weight-at-age was estimated using the coefficients from a regression of weight on length (Ricker 1975).

We used the estimated age composition, an empirical model based on temperature and growth, and an empirical model based on reproductive effort to estimate annual mortality.

We pooled the relative age frequencies for each year to generate a single catch curve and to minimize the influence of year class variation (Ricker 1975). Mortality was estimated by the regression \log_e of age frequency against age (Ricker 1975). Lines were fit variously to all ages, or segments of the curve where the slope appeared to change.

We used the relative catch (corrected for effort) of individual cohorts in each year as a second approach in estimating mortality. We estimated mortality by the regression \log_e of catch against age in the year of sampling.

We used estimates of von Bertalanffy parameters and mean reservoir temperature as parameters for an empirical model derived by Pauly (1980) to predict natural mortality. We calculated an annual mean daily temperature (11.53°C) from observations at McNary Dam (at the head of the reservoir) from

the records of the U.S. Army Corps of Engineers, Portland, Oregon. We also used measurements of gonadal somatic index (GSI) in a second model of natural mortality (Gunderson and Dygert 1988). We calculated a weighted mean GSI (as described by Gunderson and Dygert 1988) from an unpublished relationship of ripe gonad weight and female body weight in John Day Reservoir (S.Vigg, U.S. Fish and Wildlife Service, National Fishery Research Center, personal communication). The weighted mean GSI was 0.7. Northern squawfish are not considered a game fish in John Day Reservoir, and annual exploitation by anglers appears to be less than 2% (Beamesderfer et al. 1987). For that reason we assumed no fishing mortality. Estimates of natural mortality should therefore be equivalent to estimates of total mortality.

Year-Class Strength

We used the age composition of our samples to estimate relative year class strength as described by El-Zarka (1957). The procedure used a series of comparisons where the abundance of each year class was estimated relative to the preceding one in all samples where the same two cohorts were available. We developed a final index of year-class strength by standardizing mean relative abundance of each year against a single year and an overall mean of zero.

We also used a regression approach to estimate relative year-class strength from annual catch curves. We assumed that mortality was constant, and equal among all ages of five and older, and that those ages were fully recruited to the samples. We assumed mortality equal to our "best" estimate and calculated residuals for the \log_e proportion of each cohort from a simple linear regression with negative slope equal to the mortality estimate. We standardized the residuals to a mean of 0. We then calculated an "index" of year-class strength as the mean residual for a year class in all sampled years. To describe the magnitude of variation in year class abundance for our simulations we calculated the coefficient of variation from the mean and standard deviation of the index transformed as an exponent of e .

Information on the relations between year-class size and environmental conditions is lacking for cyprinids, particularly for *Ptychocheilus* spp. For that reason we used correlation analysis to examine variables possibly influencing, or related to, year-class strength in John Day Reservoir. We used seasonal data on flow, reservoir elevation, and temperature. Variables for physical correlates represented the entire year, pre-spawning, incubation, rearing, and the first winter, for the year of year-class formation (Appendix A). We used estimates of growth within year-class, and concurrent and previous year-class strength of smallmouth bass and walleye as biological correlates (Appendix A). We related both indexes of northern squawfish year class strength to each variable using the Spearman-rank nonparametric correlation procedure (Zar 1974). Because we used a large number of correlations in an exploratory fashion we did not calculate probabilities or identify statistical significance for individual correlations. We considered correlation coefficients of consistent sign (positive or negative) larger than 0.60 for both indexes of year-class strength, as evidence of a relationship between year-class strength and the variable in question. Data on flow and temperature were obtained from records of the U.S. Army Corps of Engineers,

Portland, Oregon. Growth was represented as backcalculated length-at-age. Year class strength of walleye and smallmouth bass were from Connolly and Rieman (1988) and were calculated by the method of El-Zarka (1957).

Simulations of Predation

Model Description - We used a generalized population model designed for simulation of age-structured populations (Beamesderfer 1988). The model is an adaptation of those presented by Taylor (1981) and Walters (1968), and uses inputs of growth (von Bertalanffy coefficients), age specific natural mortality and exploitation. Recruitment can be modeled as either stochastic and independent of stock, described by any hypothetical, normal distribution, or as stock dependent described by a Beverton-Holt or Ricker stock recruitment function (Ricker 1975). Output of the model provides annual summaries of total and age specific yield, numbers, production (total tissue elaboration) and recruitment. Simulations can be run for up to 250 years. The model also provides age specific weighing of any output variable. We simulated predation by squawfish as production in the population weighted by a prey-consumption-to-growth conversion efficiency. We reasoned that simulations of predator production could be used to represent expected trends in prey consumption given the appropriate conversion in each age class. We estimated the model parameters from our growth and mortality data and the best available data for other functions. We assumed natural mortality was constant with age after age 1 and operated concurrently with any mortality imposed through removals.

We did not incorporate any density dependent variation in growth or mortality after the first age class in the model. Although compensation of that sort is well known in fish (Goodyear 1980), compensation in the form of a stock dependent recruitment response is likely more important (Gulland 1978; Shepherd and Cushing 1980). Our data did not show any obvious compensation in growth based on correlations of growth and year class size. To simulate removals, we chose to represent density dependent compensation through several stock dependent reproduction models. Because little information is available describing recruitment in squawfish spp., we used three models to represent a range of possible responses (Figure 1) and bound our results. We used Beverton-Holt functions with $A = 0.5$ and $A = 0.98$ (Ricker 1975) as representations of a population with limited resilience and a population where recruitment is nearly independent of stock, respectively. We used a domed Ricker function with $a = 1.7$ (Ricker 1975) to represent a population capable of overcompensation.

In simulations assuming stock-dependent recruitment, we considered adult stock a function of adult female number and size. We calculated potential reproduction from the relative reproductive potential of each female. We assumed reproductive potential to be directly proportional to weight. Realized reproduction was a function of potential reproduction with a density dependent component expressed by the reproduction models. Survival from realized reproduction (age 0) to age 1 was standardized in all simulations to produce a stable population at an arbitrarily selected equilibrium stock size.

To simulate total food consumption and predation, we estimated a relative conversion efficiency calculated as smolts consumed/growth where both numerator and denominator are expressed in terms of ng/g of predator/day. We

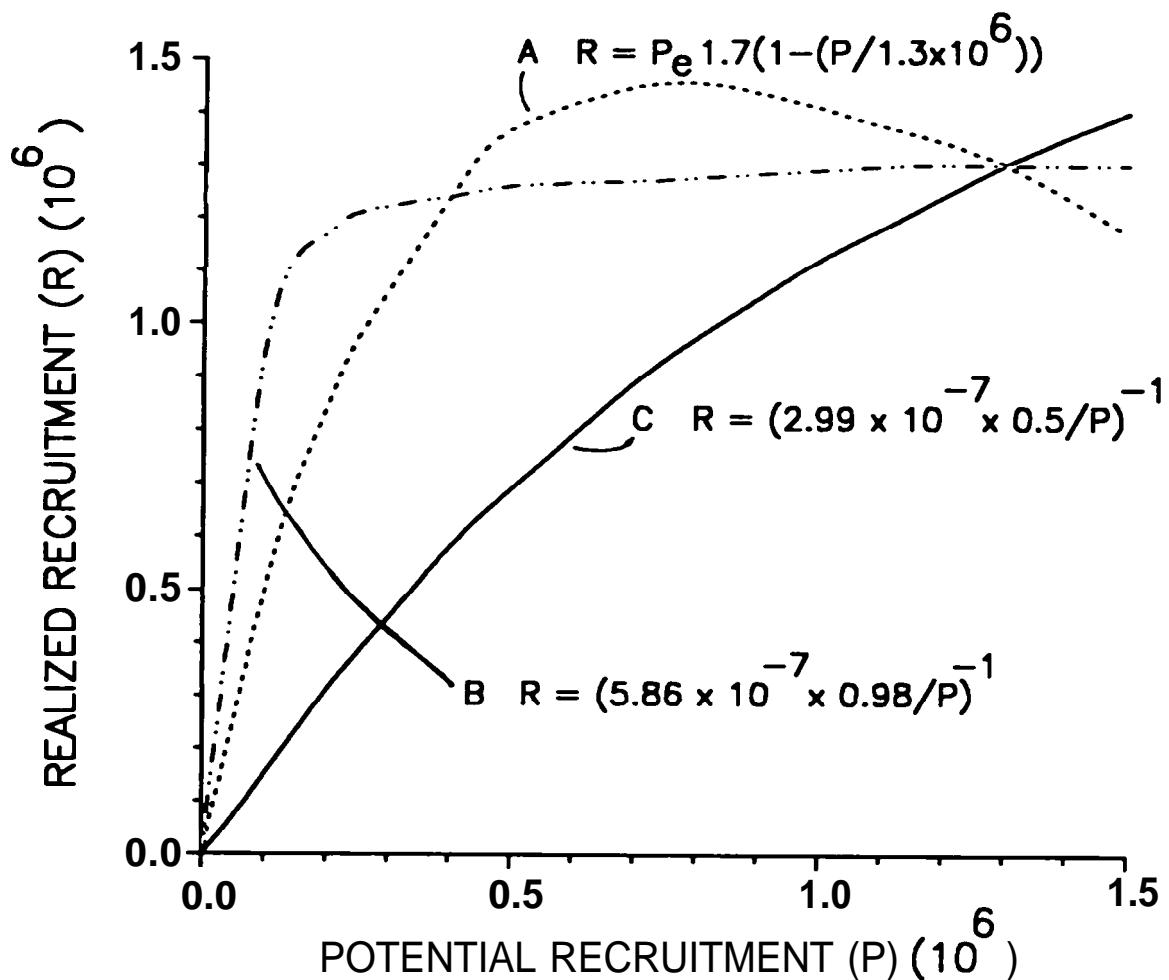


Figure 1. Reproduction models used in simulations of predation by northern squawfish in John Day Reservoir. A represents a Ricker function where $a=1.7$; B and C represent Beverton-Holt functions where $A=0.98$ and 0.50 respectively; all curves are after Ricker (1975). The arrow represents the equilibrium for all curves at 1.3×10^6 .

used empirical estimates of smolt consumption averaged from April through August (the period of smolt migration) and our estimates of annual growth. We assumed all growth occurred from April to August. Because growth may actually occur outside this period and because northern squawfish consume prey other than smolts, our estimates do not represent a true gross conversion efficiency. The factor represents only a relative conversion for smolt consumption by predators of different sizes. We assumed that caloric density of predators and prey was constant throughout the year and predicted total consumption from production on an annual basis. We averaged empirical estimates of salmonid prey consumption (Vigg et al. 1988) from all observations (over 4 years) stratified by size groups equivalent to each age class. We related estimates of conversion efficiency to size and used a regression to predict conversion efficiency for the simulations (Figure 2). We weighted annual gross production in each age class by the predicted conversion factor and summed over all ages to predict total prey consumption (potential predation) in each year of simulation. We standardized potential predation in each simulated year or age class as a proportion of total predation in an unexploited population at equilibrium

Simulations - We used our observations of year- class strength to describe potential variation in predation expected only from inherent variation in recruitment. We assumed recruitment to be independent of stock and varied it in an unexploited population, initially at equilibrium. In each year recruitment was selected from a random normal distribution. The distribution was described with a coefficient of variation equal to that from our year-class data. The simulation was run for 100 years.

We simulated the predator removals by exploiting model populations with the stock-dependent recruitment functions. We exploited each at annual rates of 0.05 to 0.80. We limited exploitation to fish larger than 275 mm, a size approximating recruitment to most gears (Beamesderfer and Rieman in press) and first maturity (Beamesderfer 1983). We projected predation at the new equilibrium as the proportion of that in an unexploited population. For simulated populations that did not reach equilibrium within 20 years we present results in that year.

We also simulated changes in predation to short term removals. Model populations were exploited at a rate high enough to reduce predation by 50% in 5 years. We then terminated removals and allowed populations to grow to equilibrium

To examine the sensitivity of our model to uncertainty in key parameters we independently varied growth (Loo in the von Bertalanffy model), mortality rate, and conversion efficiency (the slope in the conversion-length regression). We changed parameters by the range of estimates for mortality or by $\pm 25\%$ of the parameter estimate for growth and conversion. We used the Beverton-Holt model with $A=0.98$ for each simulation. We used the level of exploitation necessary to reduce potential predation to 50% of the unexploited level as the output for comparison.

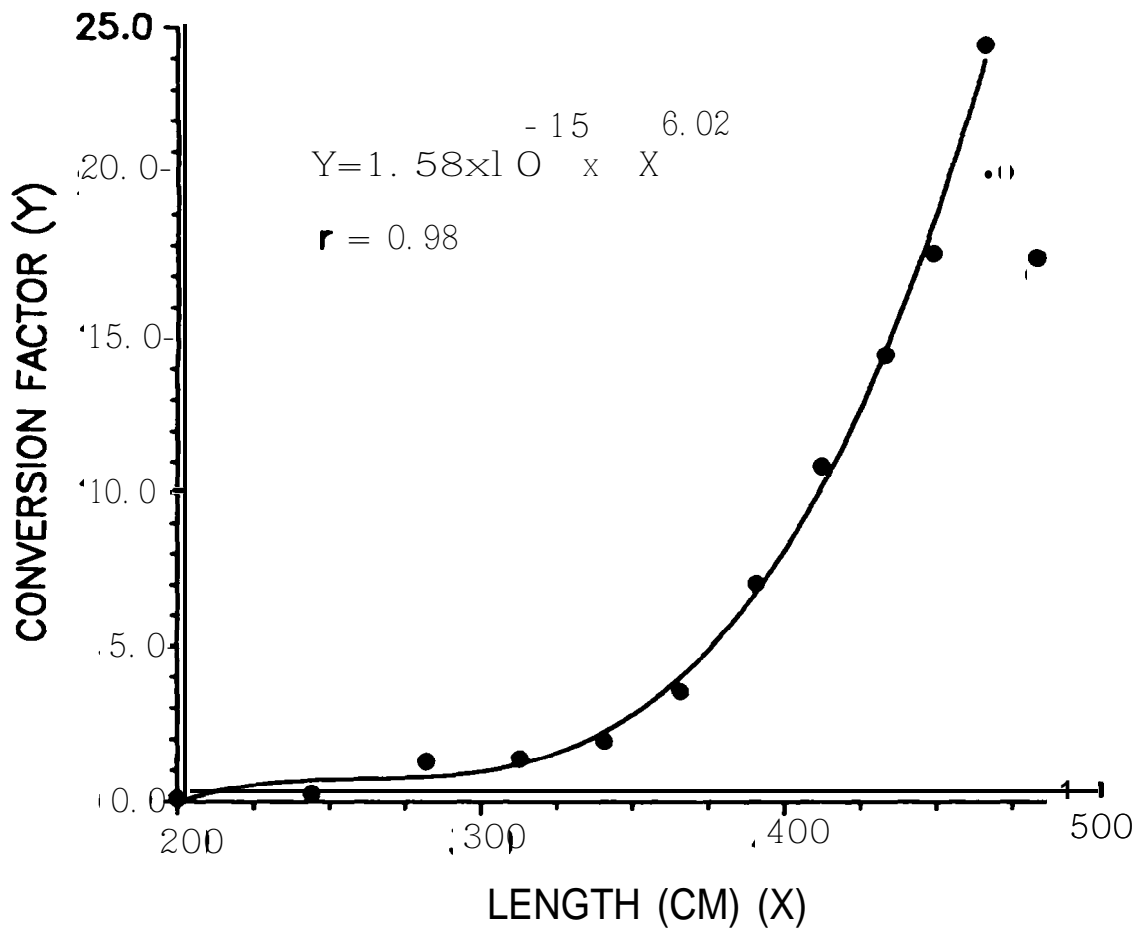


Figure 2. Relationship of prey consumption-to-growth conversions and length used in simulations of predation by northern squawfish in John Day Reservoir.

Results

Growth and Mortality

We aged northern squawfish in our samples to 16 years. The length at age we estimated for all northern squawfish in John Day Reservoir was asymptotic. We found that a von Bertalanffy model described the data well (Figure 3). Our estimates of growth were similar to or higher than those reported for other populations (Figure 3).

Our interpretation of a catch curve generated from pooled age composition data was uncertain. The right limb of the curve was not linear or smooth. Regressions fit to the data resulted in estimates of total instantaneous mortality ranging from 0.14 to 0.44 depending on the portion of the curve we used (Figure 4).

Mortality that we estimated on the basis of cohort analysis was also variable and ranged from 0.13 to 0.57. The mortality estimates did not show any age specific trend (Table 1).

Mortality estimated, using data on growth and temperature was 0.24. Mortality estimated from reproductive effort was 0.15.

Year-Class Strength

The two indexes of year-class strength for northern squawfish varied in similar fashion ($r = 0.85$) with year (Figure 5). Data converted from the catch curve index varied approximately 7 fold (coefficient of variation = 0.52). Both indexes suggested that an especially weak year class occurred in 1979. The pattern of variation did not appear to be strictly random and we did not find any strong ($r > 0.65$) or biologically meaningful correlations between either index of year class size and any of the variables representing the physical environment, fish growth, or interaction with smallmouth bass. The index of concurrent year-class size in walleye was negatively correlated ($r = -0.86; -0.67$) with both northern squawfish indexes (Figure 5). A very strong 1979 year class in walleye coincided with a weak year 1979 class in northern squawfish (Figure 5).

Simulation

Recruitment had an important influence on predation. Potential predation in a 100-year simulation where we varied recruitment randomly ranged from 57% to 165% of the mean (Figure 6). Although recruitment was varied in a random fashion in the simulation, upward and downward trends for periods of up to 10 years developed in potential predation. The coefficient of variation calculated for potential predation simulated over 100 years was 0.29 compared with 0.52 used to describe recruitment in the model.

Exploitation of northern squawfish had an important influence on potential simulated predation. Potential predation declined in exponential fashion with exploitation in each simulation, although results were dependent upon the reproduction function we used. Sustained exploitation of about 9% and 13% was necessary to reduce predation to 50% of the unexploited level with

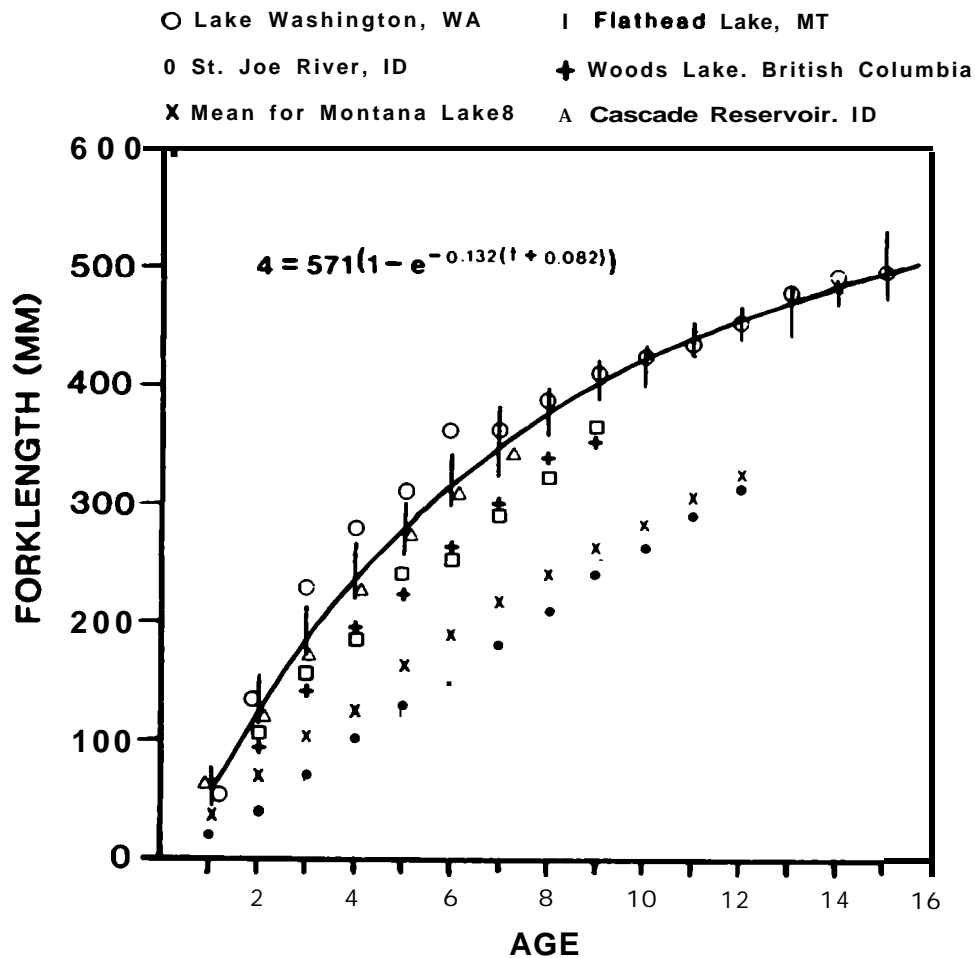


Figure 3. Backcalculated fork length-at-age for northern squawfish in John Day Reservoir. Vertical bars represent ranges of backcalculated lengths. The solid line represents the von Bertalanffy model fit to the means. The symbols represent data for other populations summarized by Beamish 1983.

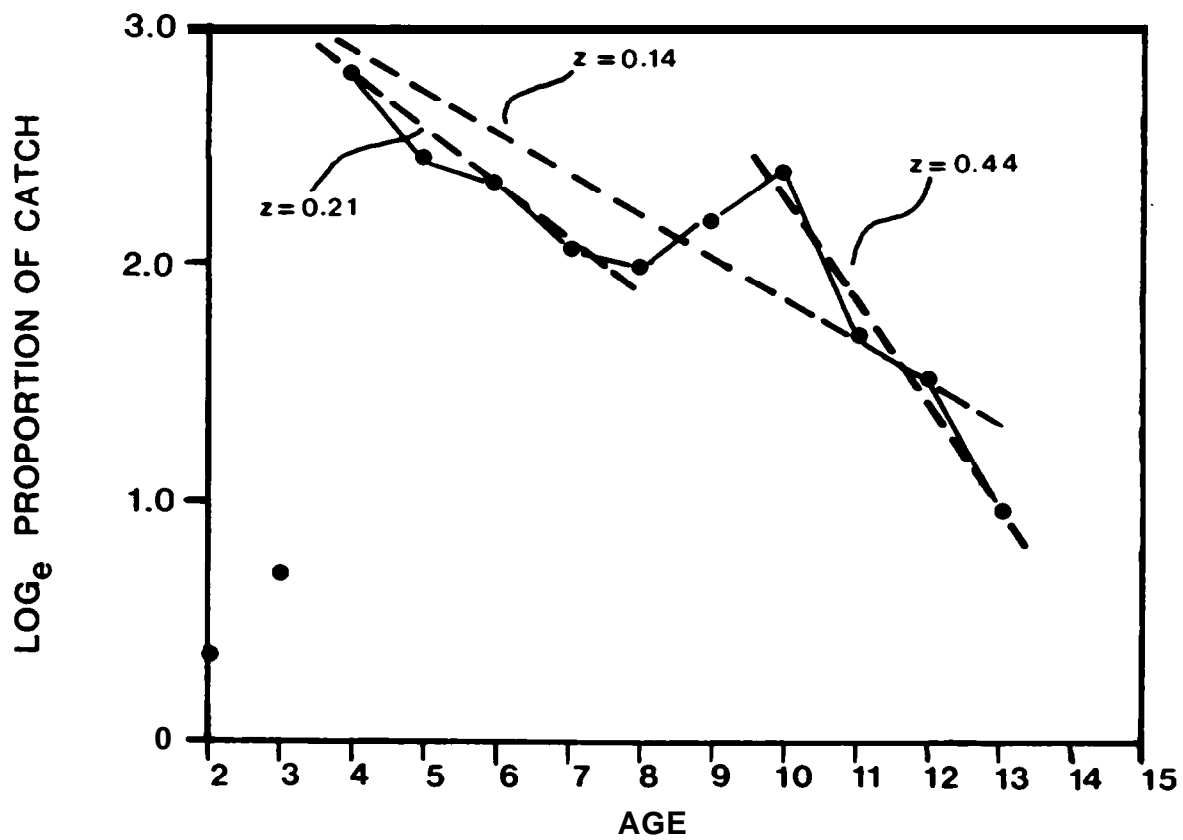


Figure 4. Catch curve for northern squawfish sampled in John Day Reservoir 1983-1986. Total instantaneous mortality (Z) estimated by regression is shown for segments of the curve indicated by the dashed lines.

Table 1. Estimated age-specific catch and mortality (total instantaneous) for individual year classes of northern squawfish in John Day Reservoir.

Year class	Age										Mortality
	5	6	7	8	9	10	11	12	13	14	
1978	103	74	96	14							0.57
1977		146	127	173	69						0.19
1976			178	126	192	91					0.16
1975				130	145	188	54				0.23
1974					129	215	105	105			0.13
1973						159	82	30	34		0.56
1972							23	53	44	10	0.27

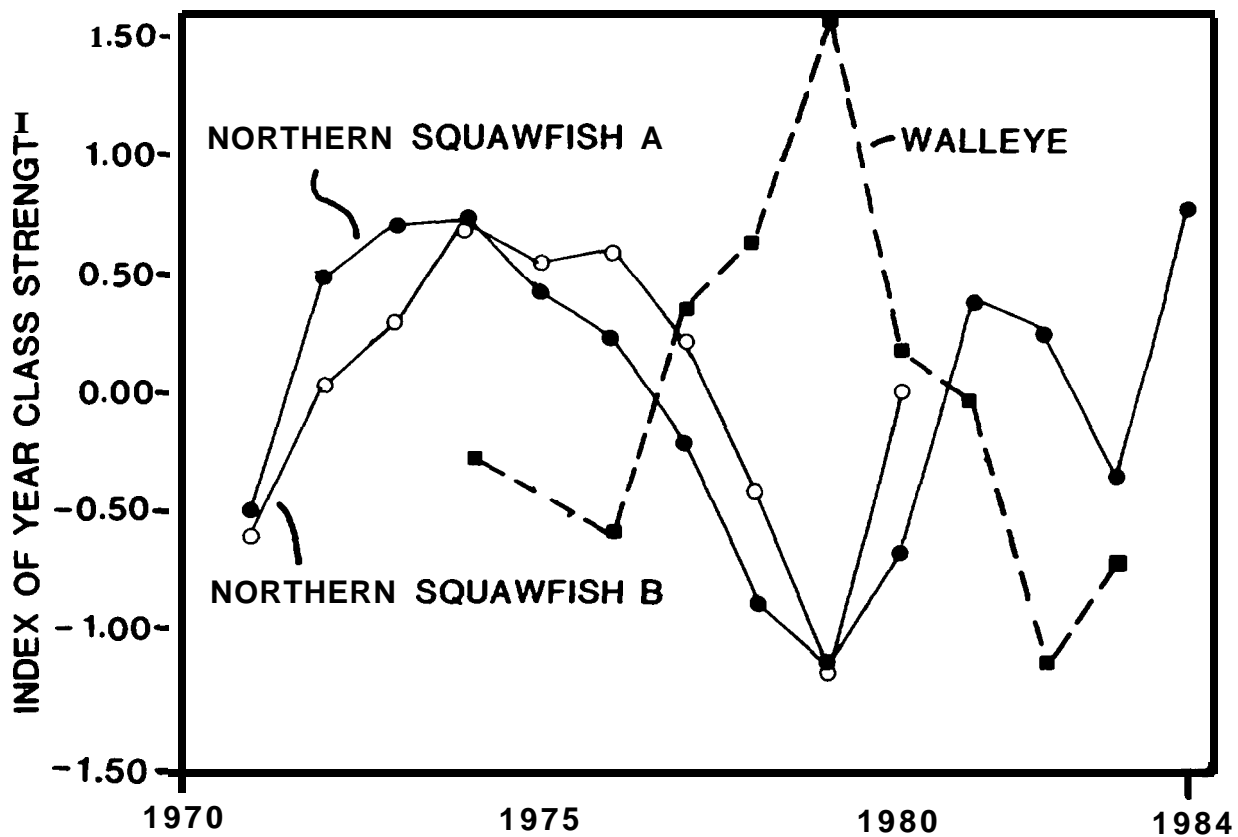


Figure 5. Indexes of relative year-class strength for northern squawfish and walleye in John Day Reservoir. A represents data for northern squawfish by the method of El-Zarka (1957), B represents data for northern squawfish by the regression method.

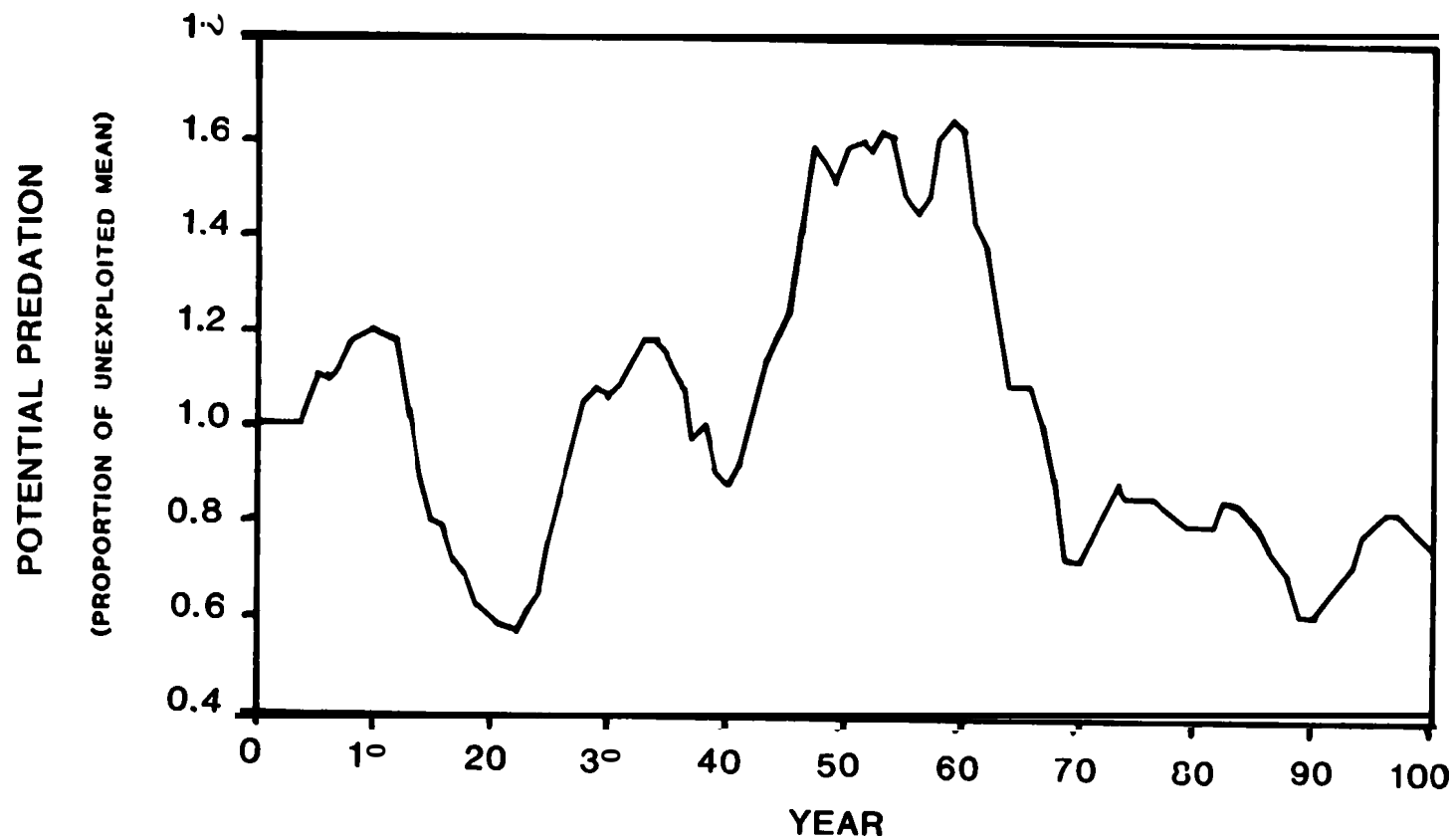


Figure 6. One hundred year simulation of potential predation by northern squawfish in John Day Reservoir. Recruitment was varied ran only, independent of adult stock.

the two "Beverton-Holt" reproduction models (Figure 7). Exploitation of 18% was necessary to achieve the same result with the domed reproduction function.

Middle and older age classes contributed most heavily to the simulated predation in unexploited populations (Figure 8). With exploitation predation declined in older ages and the relative contribution shifted toward younger fish.

The time necessary to reduce predation to 50% of the unexploited level declined rapidly with increasing exploitation in all simulations. We found that predation could be halved in 10 years with exploitation between 15% and 25%, dependent upon the reproduction model. Simulated predation was reduced by 50% within 3 years with exploitation exceeding 30% with any reproduction model.

The response of the population to a stop in exploitation was substantially different for the three simulations (Figure 9). With the least resilient reproduction model, it took nearly 30 years for potential predation to reach 90% of the unexploited level. With the other models predation reached 90% within 6 years. In the simulation using the domed reproduction model, predation exceeded (114%) the unexploited level before oscillating toward the equilibrium

The model output was not sensitive to $\pm 25\%$ change in slope of the conversion efficiency relation or a 25% increase for L_{∞} in the growth equation. The changes produced differences in the output of only $\pm 8\%$ to 12% (Table 2). The output was sensitive to a reduction in growth, where the changes produced a 108% increase in exploitation necessary to reduce predation by 50%. The range of the mortality estimates resulted in outputs ranging from +54% to -23%.

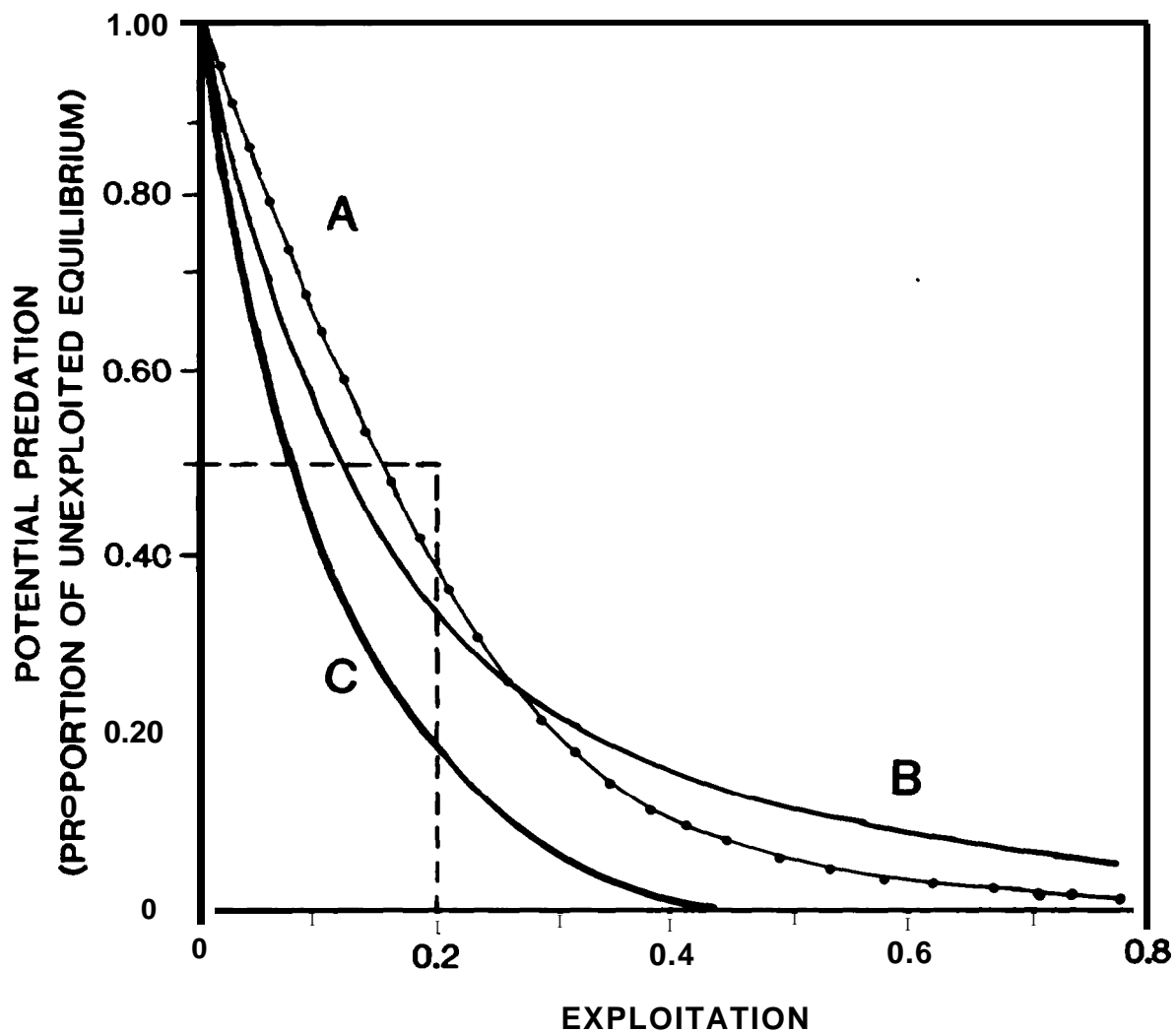


Figure 7. Simulations of potential predation by northern squawfish in John Day Reservoir with varied levels of sustained exploitation. Recruitment was modeled as a function of adult stock. A represents a simulation with the Ricker reproduction model, B and C represent simulations with Beverton-Holt models where $A=0.98$ and 0.50 respectively.

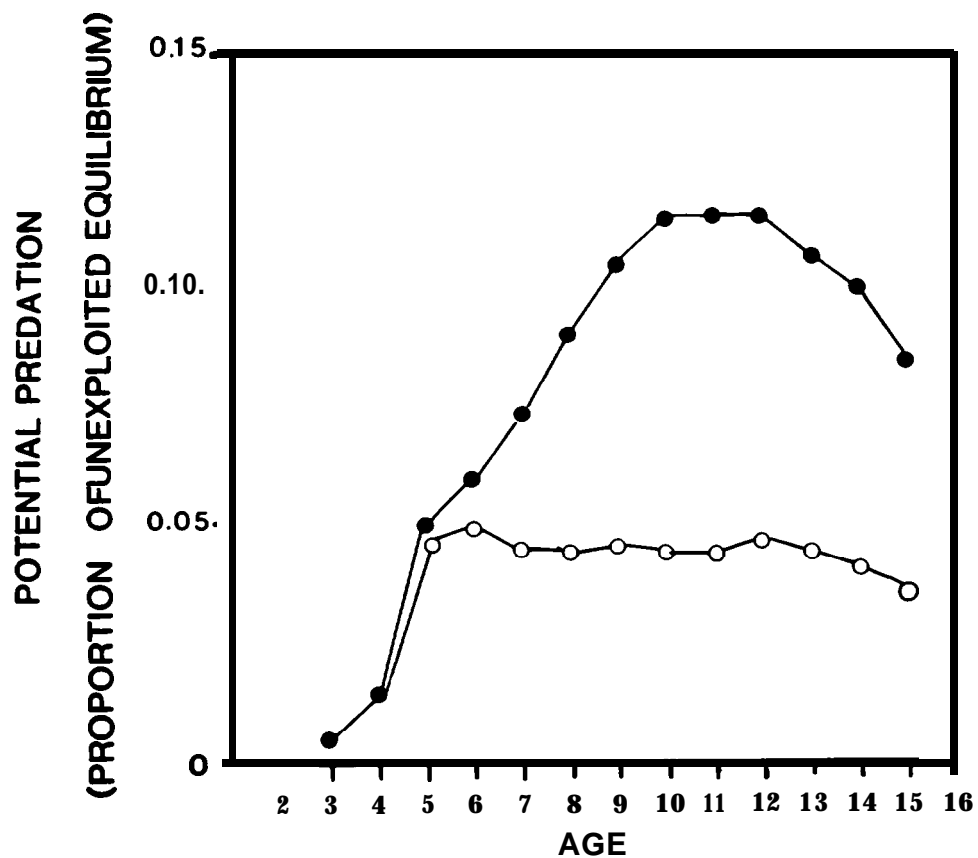


Figure 8. Simulations of potential predation by individual age classes of northern squawfish in John Day Reservoir with no exploitation and with exploitation resulting in 50% reduction of total predation.

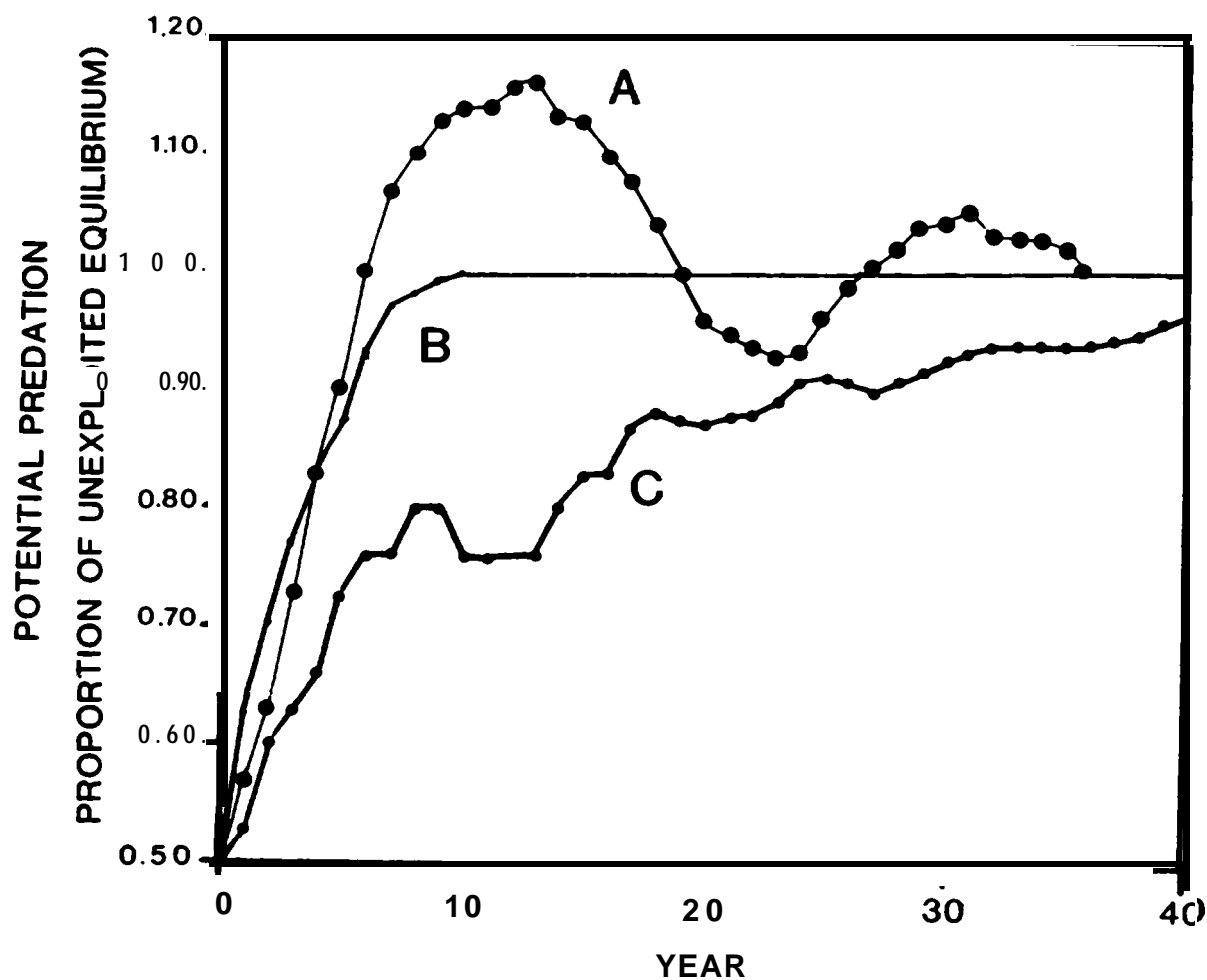


Figure 9. Simulations of potential predation following termination of exploitation on northern squawfish in John Day Reservoir. Model populations were exploited until predation was 50% of the unexploited equilibrium and then allowed to grow.

Table 2. Uncertainty of model output (exploitation resulting in a 50% reduction of simulated predation) to changes¹ in parameter estimates.

Parameter estimated	Parameter estimate	Exploitation for 50% predation
Growth (k)		
Best	57.1	0.13
Upper	71.3	0.12
Lower	42.8	0.26
Conversion efficiency¹		
Best	6.0	0.13
Upper	4.5	0.12
Lower	7.5	0.14
Mortality		
Best	0.25	0.13
Upper	0.44	0.20
Lower	0.14	0.10

¹ Growth and conversion efficiency were changed $\pm 25\%$ of the estimate, mortality was changed by the ranges of estimates.

Discussion

Our attempts to estimate mortality empirically (catch curve, cohort analysis) produced highly variable and uncertain results. The direct methods are both subject to sampling error or other bias. Variation in year class strength makes the catch curve speculative (Ricker 1975). Both methods could incorporate error from aging based on scale analysis. The variation among cohort estimates and a lack of any trend with increasing age also result in uncertainty.

The indirect estimates of mortality based on growth and temperature (0.24) and independently on reproductive effort (0.15) were relatively low. Although the empirical models used in the estimates were not developed for cyprinids they should not be discounted. These models do seem to provide good predictions of mortality across broad taxonomic boundaries (Pauly 1980; Gunderson and Dygert 1988). Our estimate based on growth was similar to mortality estimated for northern squawfish (0.27) in Lake Washington (Bartoo 1979), and the mean of our cohort estimates (0.26). For these reasons and because of the uncertainty in our direct estimates we chose 0.25 as a best approximation of average mortality for use in the simulations and year class strength analyses. For lack of better information we made the simplest assumption that mortality was constant with age after age 1. We recognized the uncertainty in the mortality estimates and used the range of estimates by each method (0.14 to 0.44) in our sensitivity analysis.

The growth of northern squawfish in John Day reservoir was on the upper range of that summarized from other populations. Growth was similar to that in Lake Washington but higher than that reported from other populations in Idaho, British Columbia and Montana (Beamesderfer 1983). The observed differences could be due to productivity of individual systems or perhaps to growing season. Both the Columbia River and Lake Washington are near sea level with moderate climates whereas other data represent populations in the intermountain region subject to shorter summers and lower temperatures over all. We found no correlation between growth of individual age classes and associated year-class strength. We found no evidence that compensation in growth was important over the range of year class sizes that we measured.

Our simulations show that variation in recruitment can have an important influence on predation. We found that potential predation in an unexploited population with varying recruitment might range more than $\pm 50\%$ through time. Trends in potential predation lasting up to 10 years were created by individually strong year classes, or by a short series of strong year classes moving through the population. The results show that inherent variation in predation can be substantial. Monitoring of predation for a management program designed to reduce salmonid mortality could be confounded by normal variation in predator populations.

Factors that influence recruitment of northern squawfish will influence predation. We did not find any correlation, however, between year-class size and physical variables of temperature, reservoir elevation, or flow. A potential to manage predation through direct manipulation of the reservoir was not obvious.

We did find negative correlations between concurrent year classes of walleye and northern squawfish. The result may represent a spurious correlation or covariation with an unidentified environmental variable that influenced each species in an opposite way. Walleye could also influence northern squawfish through predation. Young-of-the-year walleye are much larger than young-of-the-year northern squawfish (Beamesderfer et al. 1987). Walleye could easily use the young cyprinids as prey. Walleye are capable of important predation on other larval and juvenile cyprinids (Lyons 1986) and can influence year-class size of littoral zone species (Lyons 1986; Lyons and Magnuson 1987). Larval and juvenile squawfish rely heavily on a limited littoral zone in John Day Reservoir (La Bolle 1984) are probably concentrated and probably vulnerable as prey.

If walleye are important in limiting recruitment of northern squawfish, management of walleye could influence predation on salmonid smolts. Walleye are a predator on salmonids, but much less important than northern squawfish (Rieman et al. 1988). Management favoring walleye might provide a net benefit in salmonid survival. We can only speculate on the factors influencing walleye recruitment and on the interaction between walleye and northern squawfish. Although physical variables are known to influence walleye year class formation (Busch et al. 1975; Koonce et al. 1977; Serns 1982) similar relations have not been demonstrated for Columbia River stocks (Connolly and Rieman 1988). Manipulation of the reservoir environment could influence walleye and indirectly cause a net reduction of predation. More extensive knowledge on species interactions and year class formation is necessary, however, to examine such hypotheses.

Increasing mortality of northern squawfish through removal could also substantially influence predation on juvenile salmonids. Intuitively (and through our simulations) we believe that intensive (30% or more) removals of northern squawfish can reduce predation dramatically. Our belief is consistent with the logic behind many intensive control efforts. Foerster and Ricker (1941) showed that survival and production of juvenile sockeye salmon increased dramatically with removal of northern squawfish in Cultus Lake, British Columbia. Similar results have been suggested in other eradication experiments (Pintler and Johnson 1958; Jeppson and Platts 1959; MacPhee and Reid 1971) but documentation is limited. Some work indicates that removal of squawfish spp. did not benefit salmonids (Hamilton et al. 1970; Pollard 1972; Moyle et al. 1983). However, whether predation by squawfish was actually important or whether removals were significant in these studies is not clear.

We also show that reductions in predation are possible with limited (10% to 20%) but sustained removal of northern squawfish. The disproportionate effect is a result of mortality compounded through multiple age classes and a pronounced reduction in prey consumption by older fish.

We found that potential predation declined with sustained exploitation in all simulations. However, the benefit realized from exploitation was dependent on the reproduction model. Exploitation necessary for a 50% reduction in predation ranged about two fold between simulations with the least resilient Beverton-Holt model ($A = 0.50$) and the Ricker model. Even with that range, however, we considered the exploitation necessary for a significant reduction in predation to be low.

The difference in simulated predation following a stop in exploitation is a more important uncertainty. We show that the benefit from exploitation can be long term (40 year recovery) if the population is not resilient (Beverton-Holt $A = 0.50$). On the other hand, predation could rebound quickly (5 year recovery) if the population is more productive. In simulations with the Ricker model, a drop in exploitation actually resulted in over-compensation and predation exceeding the equilibrium. The rapid response was caused by replacement of juveniles through strong recruitment and by a shift in the age structure of the population with exploitation. Because size at first prey consumption and size vulnerable to exploitation were similar, and because recruitment was nearly stable or enhanced through exploitation, potential predators were "stock-piled" in age classes below those being exploited. When removals stopped those fish quickly became effective predators.

The result suggests some risk in a control program that is not sustained. Obviously the response is dependent upon reproduction and recruitment in an exploited population. We selected a domed function only to illustrate possible trends. The reproductive response in northern squawfish could be more resilient than that in our simulations. In that case the increase in predation would be greater than that shown here.

Little information addresses the reproductive response of northern squawfish. None of the large removal experiments suggest that northern squawfish populations showed any density-dependent response (Foerster and Ricker 1941; Jeppson and Platts 1959; Hamilton et al. 1970; MacPhee and Reid 1971; Pollard 1912; Beach 1974), but apparently none of the studies were maintained for more than 5 or 6 years and none monitored the dynamics of the populations. Moyle et al. (1983) does suggest that a population of Sacramento squawfish (*Ptychocheilus grandis*) recovered within 10 years following removals in a California river. The authors felt these fishes were adapted to repopulation following catastrophic events. Removal experiments with another cypriniformes, the white sucker *Catostomus commersoni*, produced some compensation in growth (Parker 1958) and recruitment (Johnson 1977). In most, eradication programs, however, no reproductive compensation was found (Trippel and Harvey 1987).

We can hypothesize the reproductive response for northern squawfish from other information. Resilient populations of fish (e.g. with domed recruitment functions) are associated with high fecundities (Colby and Nepzy 1981; Cushing 1971; Cushing and Harris 1973), strong density dependent responses in growth and mortality (Harris 1975); and with fast growing, relatively short lived species known as *r* strategists on the theoretical *r-k* continuum (Adams 1980). Fecundity for northern squawfish, ranging from 6,000 to 70,000 eggs per females (Cartwright 1956; Casey 1962; Olney 1975), is one to two orders of magnitude less than fecundities for stocks Cushing (1971) considered resilient. Growth of northern squawfish in John Day was high relative to other stocks. Growth also was not correlated with year class size. Density dependent growth was not obvious and even better growth with a population reduction should not be expected. Northern squawfish grow slowly, and exhibit relatively low mortality compared with other species. Population characteristics of northern squawfish are not those considered representative of an *r* strategist. We should not expect a resilient reproductive response.

We believe, then, that the range of reproduction functions used in our simulations bound the trends expected in northern squawfish predation. Some risk exists that compensation could aggravate predation, but the risk is probably not greater than that shown in our simulations.

We believe limited but sustained exploitation represents a better alternative for northern squawfish control than intensive removals or eradication. Radical removals are probably socially or environmentally unacceptable, or just too difficult. Large scale eradications in other areas have been attempted with toxicants and explosives (Jeppson 1957; Jeppson and Platts 1959; MacPhee 1969; Myle et al. 1983) and similar approaches have been considered on the Columbia River (Rulifson 1984). The Columbia River is a multistate and multicomunity water source and environmental concerns surround the use of toxicants (Franklin Young, Oregon Department of Fish and Wildlife, personal communication). Impacts on other valuable fishes are possible with any nonselective approach. Intensive removals with nets and traps have been successful in small systems (Foerster and Ricker 1941, Hamilton et al. 1970). Removal of large numbers spread over reservoirs as large as John Day (21,000 ha) or the entire Columbia River Basin, however, could be a difficult task. Trapping and angling techniques are effective on northern squawfish. Selective fisheries are possible on a limited scale. A selective fishery could probably produce exploitation on the order of 20% if management could develop the necessary effort in an economical way. An approach might be to develop a subsidized or self-sustaining commercial fishery. A market, the interest, and the economics of a potential fishery are yet to be analyzed. The approach is appealing, however, because at least some of the cost of a long-term control program could be generated from yield.

If a fishery were adopted, managers might find themselves in the dilemma of managing for a sustained yield and for a significant reduction in numbers. Our simulations suggest that these are compatible objectives. In all simulations, exploitation that produced maximum yield also approximated the level that produced a 50% reduction in simulated predation.

Important uncertainties exist in our analysis. Even though potential predation was reduced with exploitation, resilience in the population could represent a risk in short term control programs. In addition to our reproduction functions, our analysis relied on several other simplifying assumptions. We assumed no compensation in growth or mortality of exploited northern squawfish. Cushing and Harris (1973) and Gulland (1978) emphasize that compensation in reproduction and yearling recruitment is more important to production in exploited populations than compensation in growth or mortality of post-juvenile fish. The recruitment function we used should outweigh any compensation in growth and mortality, but the magnitude of change could be different. Although we believe strong compensation is unlikely, benefits to a control program could be less than anticipated.

The uncertainty of the model to a reduction in growth shows that an overestimate of growth could lead to an overestimate of the benefit from control. Scale analysis has a subjective component and error is possible. However, if our mortality estimates are realistic, growth must approach our estimate for fish to reach the sizes we observed. Our results do suggest that benefits from exploitation may not be the same among all populations.

The model was also sensitive to uncertainty in our mortality estimates. The uncertainty was not enough to alter our conclusion regarding the effects of exploitation, however. Results were within those bounded by our uncertainty in the reproduction response.

We also assumed that consumption of salmonids by individual predators remains constant with changing predator abundance. Peterman and Gatto (1978) suggested that change in the functional response of predators could compensate for their removal. The nature of the functional response for John Day squawfish is unclear, but present work (Vigg 1988) and further research may be helpful.

Our analysis was limited to a single predator and did not consider the potential for any response in the fish community. To reason that a reduction in predation by squawfish would result in a reduction of total predation we must assume that no other predators compensate for the loss of northern squawfish. In natural and complex communities, that type of compensation is expected (Campbell 1979; Larkin 1979). In the Columbia River reservoirs northern squawfish represent the only important salmonid predator native to the system. Other predators including walleye, smallmouth bass and channel catfish *Ictalurus punctatus* are introduced. Interactions among members of the native and introduced community are not predictable.

Our objective in this analysis was to examine management alternatives and illustrate possible responses in predation given some basic information about the dominant predator population. Our results suggest that important changes in predation could be made by manipulating recruitment or mortality in the northern squawfish population. Our approach has important limitations, and some risk is present. Further research can address some of these limitations. However, because of the economic and social importance of Columbia River salmonids and their apparent limitation by predation, control programs may be undertaken in the near future. Any such effort should include research to document compensation in predator populations and the fish community. Any evaluation of a control program should also be designed to isolate the effects of an experiment from inherent variation in the system.

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References

- Adams, P.B. 1980. Life history patterns in marine fishes and their consequences for fisheries management. Fishery Bulletin 78:1-12.

- Bagenal, T.B., and F.W. Tesch. 1978. Age and growth. Pages 101-136 in T. Bagenal, editor. Methods for assessment of fish production in freshwater. Blackwell Scientific Publications, Oxford, England.
- Bartoo, N.W. 1977. Population parameter estimates and energy budgets for peamouth, northern squawfish and yellow perch in Lake Washington. Doctoral dissertation. University of Washington, Seattle.
- Beach, D.R. 1974. Squawfish control in Cascade Reservoir. Idaho Department of Fish and Game, Performance Report, Federal Aid Project F-53-R-9, Boise.
- Beamesderfer, R.C. 1983. Reproductive biology, early life history and microhabitat of northern squawfish (*Ptychocheilus oregonensis*) in the St. Joe River, Idaho. Master's thesis. University of Idaho, Mscow.
- Beamesderfer, R.C. 1988. MDCPOP: A flexible simulator for analysis of age-structured populations and stock-related functions. Oregon Department of Fish and Wildlife, Research and Development Section Informational Report, Corvallis.
- Beamesderfer, R.C., and B.E. Rieman (In press). Size selectivity and bias in estimates of population parameters of smallmouth bass, walleye and northern squawfish in a Columbia River reservoir. North American Journal of Fisheries Management.
- Beamesderfer, R.C., B.E. Rieman, J.C. Elliott, A.A. Nigro, and D.L. Ward. 1987. Distribution, abundance, and population dynamics of northern squawfish, walleye, smallmouth bass, and channel catfish in John Day Reservoir, 1986. Annual Report to Bonneville Power Administration (Contract DE-AI79-82BP35097), Portland, Oregon.
- Brown, L.R., and P.B. Moyle. 1981. The impact of squawfish on salmonid populations: A review. North American Journal of Fisheries Management 1:104-111.
- Busch, W.N., R.L. Scholl, and W.T. Hartman. 1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie 1960-70. Journal of the Fisheries Research Board of Canada 32:1733-1743.
- Campbell, P.K. 1979. Predation principles in large rivers: A review. Pages 181-192 in H. Clepper, editor. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D.C.
- Cartwright, J.W. 1956. Contributions to the life history of the northern squawfish (*Ptychocheilus oregonensis* Richardson). Bachelor's thesis. University of British Columbia, Vancouver.
- Casey, O.E. 1962. The life history of the northern squawfish in Cascade Reservoir. Master's thesis. University of Idaho, Mscow.

- Colby, P.J., and S.J. Nepzy. 1981. Variation among stocks of walleye (*Stizostedion vitreum vitreum*): management implications. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1814-1831.
- Connolly, P.J., and B.E. Rieman. 1988. Population dynamics of walleye and smallmouth bass and potential predation on juvenile salmonids in a mainstem Columbia River Reservoir. In: T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final report (Contract DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Cushing, D.H. 1971. The dependence of recruitment on parent stock in different groups of fishes. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* 33:340-362.
- Cushing, D.H., and J.G.K. Harris. 1973. Stock and recruitment and the problem of density dependence. *Rapports et Proces-verbaux des Reunions, Conseil International pour l'Exploration de la Mer* 164:142-155.
- Ebel, W. 1977. Major passage problems. Pages 33-39 in: E. Schwiebert, editor. Columbia River salmon and steelhead. American Fisheries Society Special Publication 10, Washington, D.C.
- El-Zarka, S.E. 1957. Fluctuations in the population of yellow perch, *Perca flavescens* (Mitchill) in Saginaw Bay, Lake Huron. U.S. Fish and Wildlife Service Fishery Bulletin 151.
- Everhart, W.H., A.W. Eipper, and W.D. Youngs. 1975. Principles of fishery science. Cornell University Press, Ithaca, New York.
- Foerster, R.E., and W.E. Ricker. 1941. The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus Lake. *Journal of the Fisheries Research Board of Canada* 5:315-336.
- Francis, R.C. 1986. Two fisheries biology problems in west coast ground fish management. *North American Journal of Fisheries Management* 6:453-462.
- Goodyear, C.P. 1980. Compensation in fish populations. Pages 243-280 in: C.H. Hocutt and J.R. Stauffer, Jr., editors. Biological monitoring of fish. Heath and Company, Lexington, Kentucky.
- Gulland, J.A. 1978. Fishing, fish, and food production. Pages 387-402 in: S.D. Gerking, editor. Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford, England.
- Gunderson, D.R., and P.H. Dygert. 1988. Reproductive effort as a predictor of natural mortality rate. *Journal du Conseil, Conseil International pour l'Exploration de la mer* 39:175-192.
- Hamilton, J.A.R., L.O. Rothfus, M.W. Erho, and J.D. Remington. 1970. Use of a hydroelectric reservoir for the rearing of coho salmon. Washington Department of Fisheries Research Bulletin 9. Olympia.

- Harris, J.G.K. 1975. The effect of density-dependent mortality on the shape of the stock and recruitment curve. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* 36:144-149.
- Haynes, C.M., T.A. Lytle, E.J. Wick, and R.T. Mith. 1984. Larval Colorado squawfish (*Ptychocheilus lucius* Girard) in the upper Colorado River basin, Colorado 1979-1981. *The Southwestern Naturalist* 29:21-33.
- Jearld, W.E. 1983. Age determination. Pages 301-323 in L.A. Nielson and D.L. Johnson, editors. *Fisheries techniques*. American Fisheries Society, Bethesda, Maryland.
- Jeppson, P. 1957. The control of squawfish by use of dynamite, spot treatment, and reduction of lake levels. *Progressive Fish Culturist* 19:168-171.
- Jeppson, P.W., and W.S. Platts. 1959. Ecology and control of the Columbia squawfish in northern Idaho lakes. *Transactions of the American Fisheries Society* 88:197-202.
- Johnson, F. 1977. Responses of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations to removal of white sucker (*Catostomus commersoni*) from a Minnesota Lake, 1966. *Journal of the Fisheries Research Board of Canada* 34:1633-1642.
- Koonce, J.F., T.B. Bagenal, R.F. Carline, K.E.F. Hokanson, and N. Nagiec. 1977. Factors influencing year-class strength of percids: a summary and a model of temperature effects. *Journal of the Fisheries Research Board of Canada* 34: 1900-1909.
- La Bolle, L.D. 1984. Importance of the upper littoral zone as a rearing area for larval and juvenile fishes in a Columbia River impoundment. Master's thesis. Oregon State University, Corvallis.
- Larkin, P.A. 1979. Predator-prey relations in fishes: an overview of the theory. Pages 13-20 in H.C. Clepper, editor. *Predator-prey systems in fisheries management*. Sport Fishing Institute, Washington, D.C.
- LeCren, E.D. 1960. The efficiency of reproduction and recruitment in freshwater fish. Pages 283-302 in E.D. LeCren and M.W. Holdgate, editors. *The exploitation of natural animal populations*. Blackwell Scientific Publications, Oxford, England.
- Lyons, J. 1986. Prey choice among piscivorous juvenile walleye (*Stizostedion vitreum vitreum*). *Canadian Journal of Fisheries and Aquatic Sciences* 44:745-764.
- Lyons, J., and S.S. Magnuson. 1987. Effects of walleye predation on the population dynamics of small littoral-zone fishes in a northern Wisconsin lake. *Transactions of the American Fisheries Society* 116:29-39.

- MacPhee, C. 1969. The effect of squawfish eradication on trout survival. Pages 209-218 in Proceedings of the Forty-ninth Annual Conference of Western Association of State Game and Fish Commissioners.
- MacPhee, C., and G.E. Reid. 1971. Impact of northern squawfish on survival of fingerling rainbow trout. Idaho Department of Fish and Game, Performance Report, Federal Aid Project F-53-R-9, Boise.
- Mytle, P.B., B. Vondracek, and G.D. Grossman. 1983. Responses of fish populations in the North Fork of the Feather River, California to treatments with fish toxicants. North American Journal of Fisheries Management 3: 48-60.
- Nigro, A.A., and six coauthors. 1985. Abundance and distribution of walleye, northern squawfish, and smallmouth bass in John Day Reservoir, 1985. Annual report (Contract DE-AI79-84BP35097) to Bonneville Power Administration Portland, Oregon.
- Olney, F.E. 1975. Life history and ecology of the northern squawfish, *Ptychocheilus oregonensis*, in Lake Washington. Master's thesis. University of Washington, Seattle.
- Parker, R.A. 1958. Some effects of thinning on a population of fishes. Ecology 39: 304-317.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperatures in 175 fish stocks. Journal du Conseil, Conseil International pour l'Exploration de la Mer 39: 175-192.
- Peterman, R.M., and M. Gatto. 1978. Estimation of functional responses of predators on juvenile salmon. Journal of the Fisheries Research Board of Canada 35: 797-808.
- Pintler, H.E., and W.G. Johnson. 1958. Chemical control of rough fish in the Russian River drainage, California. California Fish and Game 44: 91-124.
- Pollard, H.A. 1972. Squawfish control in Anderson Ranch Reservoir. Idaho Department of Fish and Game, Completion Report, Federal Aid F-53-R-7, Boise, Idaho.
- Raymond, H.L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966-1975. Transactions of the American Fisheries Society 108: 505-529.
- Raymond, H.L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River Basin. North American Journal of Fisheries Management 8: 1-24.
- Ricker, W.E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11: 559-623.

- Ricker, W.E. 1963. Big effects from small causes: two examples from fish population dynamics. *Journal of the Fisheries Research Board of Canada* 20: 257- 264.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191.
- Rieman, B.E., R.C. Beamesderfer, S. Vigg, and T.P. Poe. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River Reservoir: Part IV. Total loss and mortality of juvenile salmonids to northern squawfish, walleye, and smallmouth bass. In T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Rulifson, R.L. 1984. Investigation of the process for registration of squoxin for squawfish control. Final Report (Contract DE-AI83-BP13220) to Bonneville Power Administration, Portland, Oregon.
- Shepherd, J.G., and D.H. Cushing. 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* 39:160-167.
- Serns, S.L. 1982. Influence of various factors on density and growth of age-0 walleyes in Escanaba Lake, Wisconsin, 1958-1980. *Transactions of the American Fisheries Society* 111:299-306.
- Taylor, M.W. 1981. A generalized inland fishery simulator for management biologists. *North American Journal of Fisheries Management* 1:60-72.
- Trippel, E.A., and H.H. Harvey. 1987. Reproductive responses of five white sucker populations in relation to lake acidity. *Canadian Journal of Fisheries and Aquatic Sciences* 44:1018-1023.
- Vigg, S. 1988. Functional response of northern squawfish predation to salmonid prey density in McNary Tailrace, Columbia River. In T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Walters, C.J. 1969. A generalized computer simulation model for fish population studies. *Transactions of the American Fisheries Society* 98:505-512.
- Zar, J.H. 1984. *Biostatistical analysis*. Second Edition. Prentice-Hall, Englewood Cliffs, New Jersey.

Appendix A

Variables used in correlations with two indexes of northern squawfish year-class strength

Variable and period represented ¹
Walleye year-class
Previous year
Concurrent year
Smallmouth bass year-class
Previous year
Concurrent year
Length at age
Age 1
Age 3
Mean daily flow
May
June
July
August
March-May Inclusive
May-June Inclusive
June-August Inclusive
January-December Inclusive
Degree days
November-March Inclusive (following spawning)
Mean daily temperature
May
June
July
August
March-May Inclusive
May-June Inclusive
June-August Inclusive
Rate of temperature increase (°C/day) ²
May
June
July
August

Appendix A (continued).

**Variable and
period represented¹**

Mean daily reservoir elevation

**My
June
July**

Standard deviation of reservoir elevation

**My
June
July
August**

¹ **Periods were selected to represent prespawning, spawning, incubation or rearing. Spawning is in June.**

² **Rate of increase was estimated by regression.**

Population Dynamics of Walleye and Smallmouth Bass and
Potential Predation on Salmonid Smolts in
John Day Reservoir

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Abstract

We described potential predation on salmonid smolts (*Oncorhynchus* spp. and *Salmo gairdneri*) as a function of the population dynamics of walleye *Stizostedion vitreum vitreum* and smallmouth bass *Micropterus dolomieu* in John Day Reservoir of the Columbia River. Walleye and smallmouth bass grew well in John Day Reservoir relative to other populations in northern USA and southern Canada. Our best estimates of total instantaneous mortality were 0.60 for walleye and 0.50 for smallmouth bass. Year-class strength was much more variable for walleye than smallmouth bass. Walleye year-class strength was correlated negatively with annual mean flow and correlated positively with higher water level in March and higher water temperature during June through August. Year-class strength of smallmouth bass was not strongly correlated with any environmental variable. Strength of walleye and smallmouth bass year classes were correlated positively with length at age 1. The relative importance of walleye and smallmouth bass as predators of salmonid smolts changed with structure of the populations. Predation was characterized by early participation of walleye and smallmouth bass, but was short-lived because consumption of smolts and predator number declined quickly with age. Since a short lag period existed before predation on smolts began, variation in year-class strength of walleye and smallmouth bass rapidly affected predation. Simulated interactions of exploitation and size limits for walleye and smallmouth bass did not strongly influence predation except at higher than reported rates of exploitation and smaller than desirable sizes at harvest. Promotion of a better fishery for walleye and smallmouth bass should not conflict with management of salmonids, but management for increased recruitment of walleye may conflict.

Mortality of salmonid smolts (*Oncorhynchus* spp. and *Salmo gairdneri*) that pass individual hydroelectric projects of the Columbia River basin is estimated between 15% and 45% (Sims and Osslander 1981). A major portion of the estimated mortality is attributed to passage at dams (Schoneman et al. 1961; Gray and Rondorf 1986), but an estimated 9% to 19% is attributed to predation by resident fish (Rieman et al. 1988). Rieman et al. (1988) estimated that walleye *Stizostedion vitreum vitreum* and smallmouth bass *Micropterus dolomieu* accounted for 13% and 9%, respectively, of the total predation of smolts in John Day Reservoir during 1984-86. Because salmonid stocks of the Columbia River support economically important commercial and recreational fisheries in the ocean (Nicholas and Hankin 1988) and the Columbia River basin (Oregon Department of Fish and Wildlife and Washington Department of Fisheries 1987), control of predator populations has been investigated (Gray et al. 1984). Although walleye and smallmouth bass contribute a small proportion of the total predation, the relative importance of these two predators could change as the populations vary naturally through time. The need, timing, and success of controlling predation by walleye and smallmouth bass will, ultimately, be dictated by the population dynamics of these predators.

We lack published information on growth, mortality, and year-class variation of Columbia River stocks of walleye and smallmouth bass needed to predict how predation might change. We do know that environmental factors influence year-class strength of walleye (Kelso and Bagenal 1977; Koonce et al. 1977) and smallmouth bass (Christie and Regier 1973; Paragamian 1987) in other systems. We also know that recruitment often appears unrelated to density of adults in walleye (Busch et al. 1975; Forney 1976; Smith 1977; Serns 1982) and smallmouth bass (Christie and Regier 1973; Latta 1975). Intuitively, changes in abundance and population structure of a predator will cause variation in the level of smolt predation.

We believe that to fully consider management goals we must describe the variation in smolt loss to predators. Fisheries for walleye and smallmouth bass in the Columbia River basin are important. Managers must determine whether the implementation of potentially expensive measures to limit these predators would generate significant increases in adult salmon and steelhead. Conversely, managers must ask if management of recreational fisheries for walleye and smallmouth bass is compatible with a goal of improving salmon and steelhead runs in the mid and upper Columbia River drainage. In this paper we address the relative loss of juvenile salmonids as a consequence of change in populations of walleye and smallmouth bass.

Specific objectives of this study were to (1) describe the population dynamics of walleye and smallmouth bass in John Day Reservoir, (2) describe influence of environmental factors on recruitment of the two predators, (3) describe potential variation in predation on juvenile salmonids with changes in predator populations, and (4) describe opportunities for management to control predation, enhance the recreational fishery for walleye and smallmouth bass, or both.

Study Area

John Day Reservoir is one of four "run-of-the-river" impoundments operated for hydroelectric power generation and navigation on the lower Columbia River between Oregon and Washington. The reservoir is 123 km long and covers about 21,000 hectares. Offshore depths range from 10 m in the upper reservoir to 50 m near John Day Dam. The reservoir grades from a riverine to lentic character through its length, but current is measurable throughout. Hydraulic residence time ranges from 3 to about 12 days (LaBolle 1984), and daily flow pattern is regulated through McNary Dam and John Day Dam. The shoreline is typically steep, substrate is basalt, and littoral habitat is limited. Precipitation is low and shoreline vegetation is sparse. Water temperature ranges from 0° to 27°C with lows in January or February and highs in August. Juvenile salmon and steelhead are present in the reservoir all year, but most of the salmonids migrate through the system as smolts from April through August.

Methods

We used back-calculated lengths at age, age-length keys, and catch-composition data from Beamesderfer et al. (1987) to estimate growth, mortality, and variation in year-class strength of walleye and smallmouth bass from John Day Reservoir. Fish sampling and aging methods are fully described in Beamesderfer and Rieman (1988a). Data from 1,987 walleye and 7,885 smallmouth bass collected from 1983 through 1986 were used in our analyses. We used a population model to simulate effects of variation in predator recruitment and fishery management on predation of salmonid smolts. Parameter estimates for the model were based on our estimates of growth, mortality, and year-class strength. Estimates of size-related smolt consumption were derived from a companion study (Vigg et al. 1988). Walleye data were analyzed for the entire reservoir. Smallmouth bass data were partitioned by lower and upper reaches of the reservoir to derive representative populations dynamic parameters following Beamesderfer et al. (1987).

Age and growth

We used age-length keys developed by Beamesderfer et al. (1987) from backcalculated age-at-length data to convert length frequencies to age frequencies. We then adjusted catch data within each length group for differential gear vulnerability as described by Beamesderfer and Rieman (1988b). Mean length at age was determined from all fish aged. The data were fit with the von Bertalanffy model (Ricker 1975) to describe growth and estimate coefficients (i.e., L_{∞} and K). We compared our estimates of growth with those of other North America stocks of walleye and smallmouth bass.

Mortality

We used catch curves and analysis of age-specific catch by cohort (Ricker 1975) to estimate total annual mortality of walleye and smallmouth bass. To minimize influence of year-class variation, relative age-frequency data from all sampling years were pooled to produce a single catch curve (Ricker 1975).

We calculated the regression of \log_e age frequency on age to derive an estimate of mortality. We estimated mortality from annual catches of individual cohorts. We used catch data from cohorts that were sampled for three or four continuous years and fully recruited to the fishing gear. Annual mortality was calculated from the regression of \log_e catch on age for fully recruited age-classes.

Natural mortality was estimated from an empirical model by Pauly (1980). This model is based on growth and an estimate of annual mean reservoir water temperature. We used the growth coefficient, L_{∞} , from the van Bertalanffy equation and the daily mean temperature (11.5°C) recorded at McNary Dam by U.S. Army Corps of Engineers. We combined these estimates of natural mortality for walleye and smallmouth bass with values of exploitation given by Beamesderfer et al. (1987) to estimate total instantaneous mortality for each species.

Year-class strength

We used two methods to estimate relative strength of year classes. We modified the method of El-Zarka (1959) to make conservative comparisons among strength of each cohort relative to that of other cohorts over all sampling seasons. Our modification consisted of eliminating a cohort if catch of the cohort represented less than 5% of total catch within all sampling years. The El-Zarka index (El-Zarka 1959) of year-class strength was derived by standardizing the relative abundance of all cohorts to a mean of zero.

We also estimated relative year-class strength with a regression approach. We assumed stable mortality and constructed annual catch curves for walleye and smallmouth bass. We assumed that once fish were fully recruited to our sample, any deviation from a regression line calculated for catch curves would be solely due to variation in year-class strength. A single regression line was defined for each species with a negative slope equal to our best estimates of mortality. We calculated a mean of the residuals from the regression for each cohort over all sampling years. We then standardized the mean residuals to an overall mean of zero for all cohorts, and the resulting values were used as an index of year-class strength.

We used the residual index of year-class strength to make relative estimates of walleye and smallmouth bass recruited to age 1. We chose lower or upper reservoir values of year-class strength of smallmouth bass based on strength of correlation (i.e., agreement) of our regression index with the modified El-Zarka (1959) index of year-class strength. We converted the estimates of year-class strength to a multiplication factor by taking the exponential of the estimates and standardizing the new values to a mean of 1.0. We multiplied these values by estimates of mean recruitment of 15,000 for walleye and 35,000 for smallmouth bass. The mean recruitment values were arbitrary, but conformed to relative abundance estimates by Beamesderfer and Rieman (1988a).

Indexes of year-class strength were correlated with environmental and population variables identified as potentially important influences on year-class strength of walleye (Colby et al. 1979; McMahon et al. 1984) and smallmouth bass (Edwards et al. 1983). We obtained reservoir elevation,

water temperature, and flow data from the U.S. Army Corps of Engineers (Portland, Oregon). We used length-at-age 1 as a population variable to account for influence of growth and year-class strength from one year previous to account for influence of cannibalism. We related indexes of year-class strength of walleye and smallmouth bass to each variable (Appendix Tables 1-3) by the Spearman rank-correlation procedure (Zar 1974). We considered correlations to be strong if both year-class indexes had a correlation coefficient of at least ± 0.50 with the same variable.

Simulations of predation

Model description - We used a generalized population model designed for simulation of age structured populations (Beamesderfer 1988). The model is an adaptation of those by Walters (1969) and Taylor (1981). The model uses estimates of growth (von Bertalanffy coefficients K and L_{∞}), age-specific natural mortality, and exploitation provided by the user. Recruitment can be modeled as stochastic and independent of stock described by a normal distribution or as stock dependent described by a Beverton-Holt or Ricker function (Ricker 1975). The model provides annual summaries of total and age specific yield, number, production (as total tissue elaboration), and recruitment for 1 to 250 years of simulation. The model also produces age-specific weighing of individual variables from a schedule of weighing factors provided by the user.

Parameter estimates - We provided the model our best estimates of growth, mortality, and recruitment and the best available data for other functions (Appendix Table 4). We assumed that natural mortality was constant with age after age 1 and operated concurrently with any mortality imposed through removals.

To simulate predation, we estimated a relative conversion efficiency calculated as number of smolts consumed/annual gain in weight of predator where both numerator and denominator are expressed in terms of milligrams/grams predator/day. We used empirical estimates of smolt consumption averaged from April through August (the period of smolt migration). Our estimates of annual growth assumed all growth occurred from April through August. Because growth may actually occur outside this period and because walleye and smallmouth bass consume prey other than salmonid smolts, our estimates do not represent a true gross conversion efficiency. The factor represents only a relative conversion for smolt consumption by predators of different sizes. We assumed caloric density of predators and prey was constant throughout the year and predicted total consumption from production on an annual basis.

We obtained empirical estimates of daily ration of salmonid prey by walleye and smallmouth bass from Vigg et al. (1988). Vigg et al. (1988) stratified predators by size groups derived from backcalculated size-at-age estimates reported by Beamesderfer et al. (1987) and calculated daily prey

ration over four years of observations. We derived size-specific conversion efficiencies (CE) from these ration estimates by the equation

$$CE = \text{Ration} / 1,000(e^{G/d} - 1)$$

where

$$G = \ln \text{wt}_{\text{age } i+1} - \ln \text{wt}_{\text{age } i}, \text{ and}$$

d = number of days from 1 April to 31 August = 153.

We then developed a consumption function for walleye (Figure 1) and for smallmouth bass (Figure 2) by plotting conversion efficiency against mean size at age and smoothing the function where appropriate (Appendix Tables 5 and 6). We used this function to derive pertinent conversion efficiency values for size-at-age estimates defined by the von Bertalanffy model (Ricker 1975).

To predict total prey consumption (potential predation) in each year of simulation, we weighted annual gross production in each age class by the predicted conversion factor and summed over all ages. We standardized potential predation in each simulated year or age class as a proportion of total predation in an unexploited population at equilibrium

Experimental design - We used our simulations to describe variation in predation caused by variation in year-class strengths of walleye and smallmouth bass. To create a population structure similar to the real ones, we used sequential one-year simulations with individual annual recruitment varied in a pattern following that derived from our index of year-class strength. After the empirical recruitment series, the simulation was continued for an additional 100 years. During the 100-year simulation we varied recruitment in a random normal fashion with a mean and standard deviation equal to that calculated from our regression index of year-class strength. We assumed recruitment to be independent of adult stock. We assumed that simulated variation in predation over the 100-year period represented potential variation in predation by walleye and smallmouth bass populations.

We used a series of 100-year simulations to describe the sensitivity of our model to independent changes in predator rates of growth and total annual mortality. Populations were set at equilibrium and recruitment was varied in a random normal fashion with the declared mean and standard deviation developed from our index of year-class strength as above. Growth rate (K of von Bertalanffy model) and total annual mortality were constant for a simulation but were varied independently by $\pm 25\%$ among simulations. Since the model output for predation (i.e., weighted effect of production) varies directly with recruitment (Beamesderfer 1988), our final estimates of relative predation were derived by dividing simulated values for mean predation by simulated values for mean recruitment to factor out variation that was due to random differences in mean recruitment among simulations. We calculated percent change in relative predation for a simulation run using a single adjusted parameter versus a run with our best parameter estimates. We also computed the coefficient of variation (i.e., SD/mean) of relative predation for runs with adjusted and best estimate parameters. Sensitivity analysis served a dual purpose: to test for implications of error in parameter estimation and to test how the predator populations might vary under sustained habitat changes.

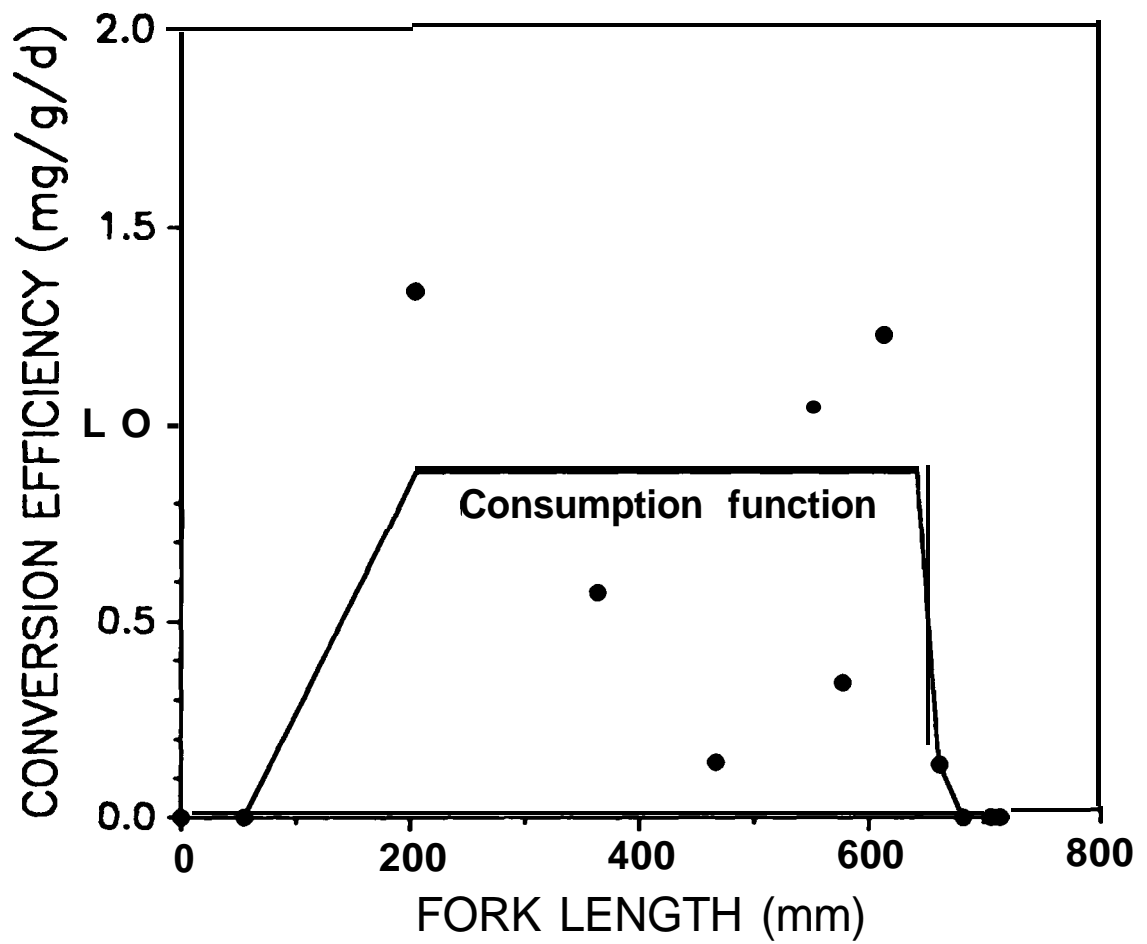


Figure 1. Length-specific food conversion efficiency and consumption function derived for walleye feeding on salmonid smolts in John Day Reservoir.

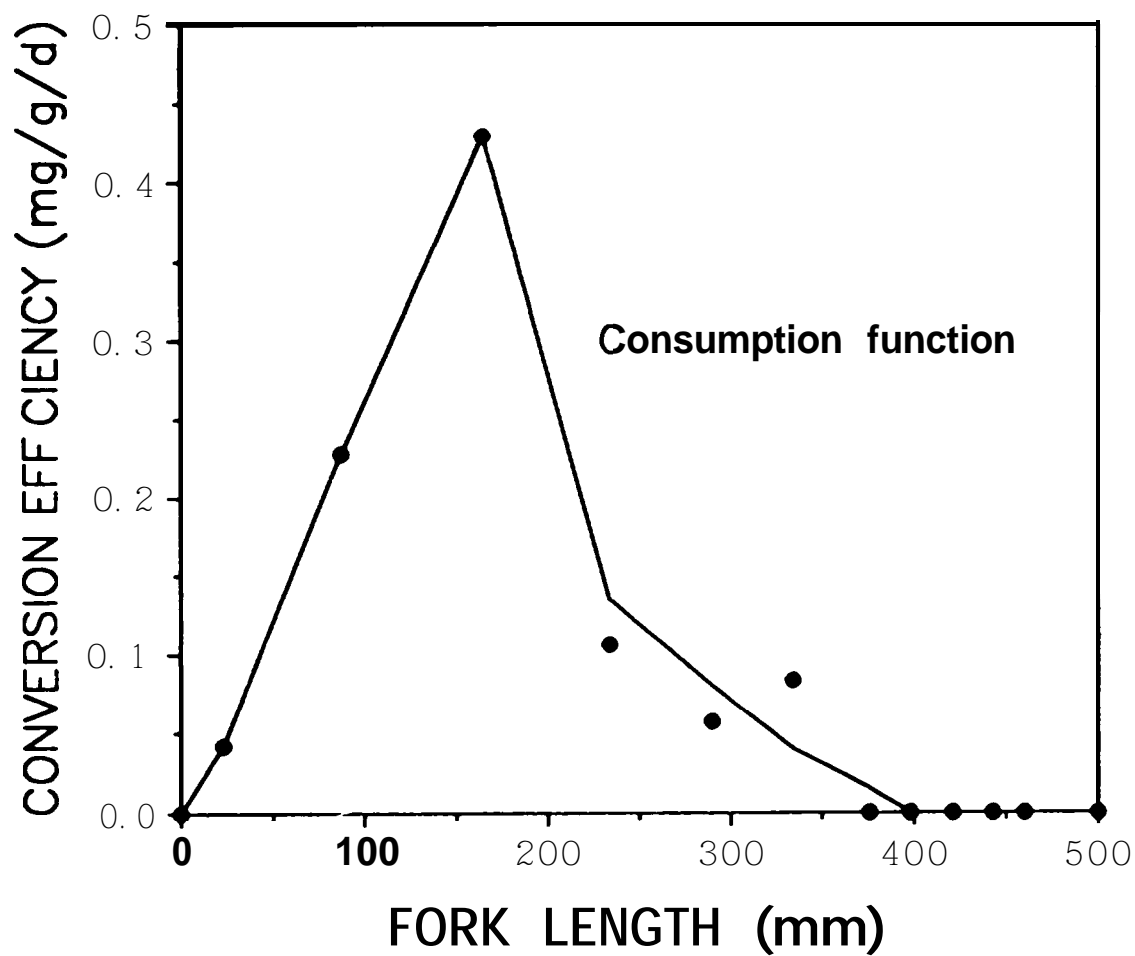


Figure 1. Length-specific food conversion efficiency and consumption function derived for smallmouth bass feeding on salmonid smolts in John Day Reservoir.

To examine the effects of fishery management on predation, we varied exploitation and size at harvest in a series of 100-year simulations. We set natural mortality equal to estimates derived from the Pauly (1980) model. We exploited model populations of walleye from 5% to 60% and smallmouth bass from 10% to 80% inclusive of the range of exploitations experienced by most fisheries. Size at harvest was varied from 10 to 18 inches for walleye and 7 to 12 inches for smallmouth bass. These include the range of sizes potentially harvested under no regulations and the commonly proposed minimum size limits.

Results

Walleye

Age and growth - Length at age data fit to a von Bertalanffy model yielded the equation: $L_t = 715 [1 - e^{-0.335(t - 0.143)}]$ Growth of walleye in John Day Reservoir was good compared with growth in other populations of walleye in northern USA and southern Canada (Figure 3).

Mortality - Mortality estimates varied with the method used. Total instantaneous mortality estimated by catch curve analysis was 0.72 for 6-9 year old walleye (Figure 4). We felt that estimating mortality for younger fish was unrealistic. Mortality estimates from cohort analysis were highly variable (Table 1). The estimate of natural instantaneous mortality from Pauly's model (Pauly 1980) was 0.45. Beamesderfer et al. (1987) previously estimated exploitation rate at 0.05 from tag return data collected in 1985-1986. Combined Pauly's model and Beamesderfer et al. (1987) estimates equated to a total instantaneous mortality of 0.50.

Year-Class strength - The two estimates of year-class strength of walleye were similar (Figure 5). The modified El-Zarka (1959) method, however, produced estimates over a wider range of year classes than the regression method. Both methods indicated that 1979 was the strongest year class for the period 1975-82 whereas 1982 was the weakest. Our estimates of relative recruitment varied 79-fold from minimum to maximum values (Table 2). The coefficient of variation for recruitment was 0.94.

Correlation between physical habitat variables and indexes of year-class strength of walleye varied with the method used to estimate year-class strength. Both methods produced strong correlations with various seasonal values of flow, reservoir level and temperature (Appendix Table 1). El-Zarka (1959) and residual indexes of year-class strength were correlated negatively with annual mean discharge ($r = -0.90$; -0.71 , respectively). Negative correlations with mean flow were stronger for summer months (June-August) than for spring months (March-May). Strong positive correlation with reservoir levels were found in March ($r = 0.70$; 0.64) and with water temperature during the whole summer ($r = 0.57$; 0.76) and during July ($r = 0.64$; 0.76). Length at age 1 was strongly correlated with year-class strength ($r = 0.85$; 0.90).

Simulations of predation - We found that predation of salmonid smolts averaged 188% higher in our 100-year simulations than that estimated for 1982

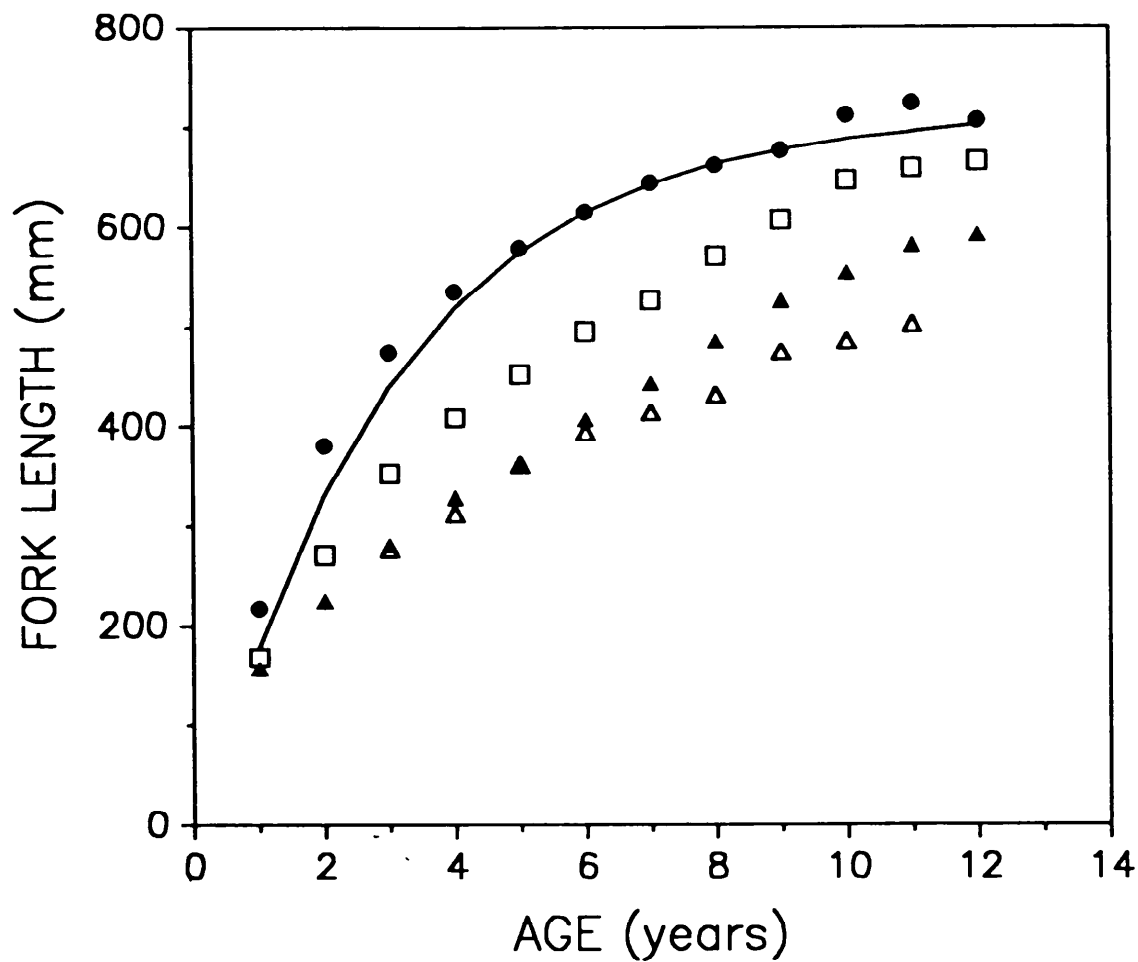


Figure 3. Comparison of growth for walleye from John Day Reservoir (●) to walleye from other waters in North America: Clear Lake, IO (□) (Carlander and Whitney 1961); Lake of the Woods, MN (▲) (Carlander 1944); and Lake Manitoba (△) (Kennedy 1949).

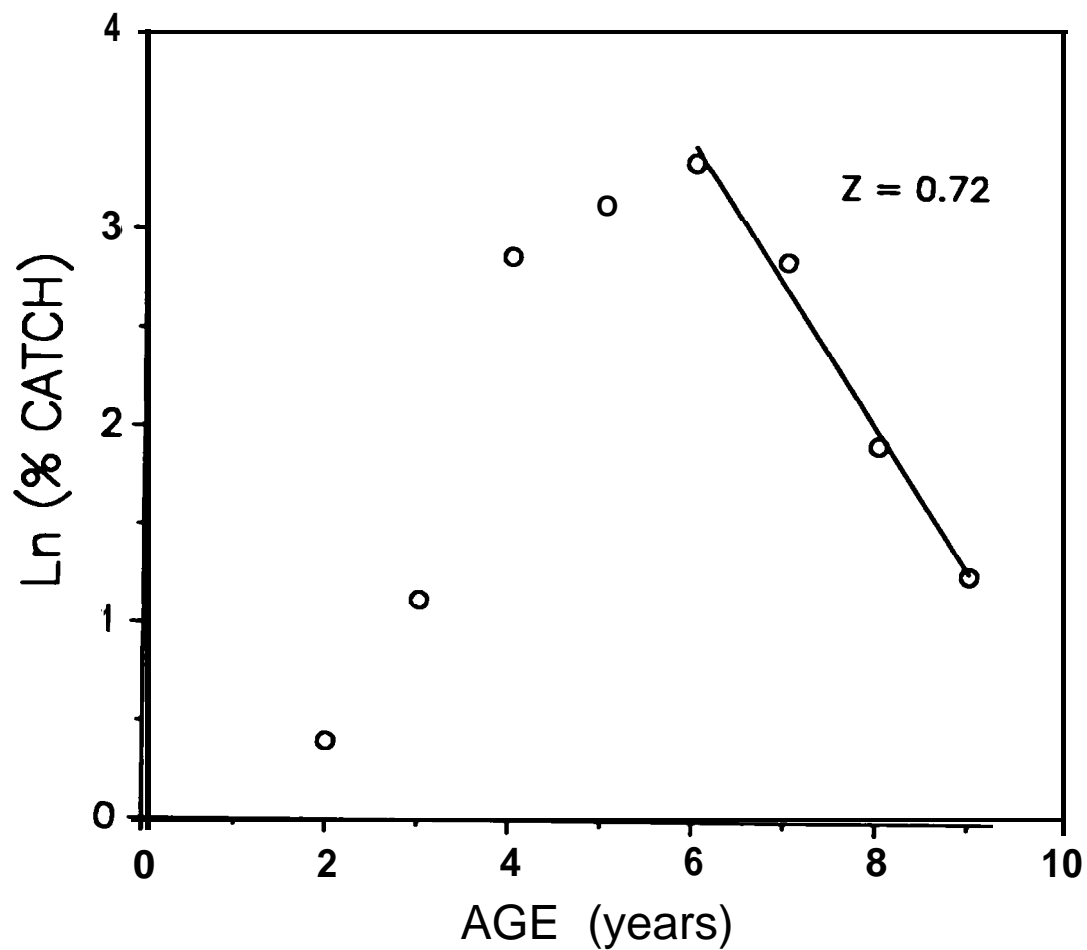


Figure 4. Catch curve for walleye in John Day Reservoir from pooled data taken in 1983-86. Annual instantaneous mortality (Z) was estimated from a regression line of data for age 6-9 year old walleye.

Table 1. Age-specific catch and estimated mortality (total instantaneous) for three year classes of walleye in John Day Reservoir.

Year class	Catch at age				Mortality
	6	7	8	9	
1977	--	1,426	829	527	0.50
1978	1,691	2,006	953	--	0.29
1979	7,202	3,056	--	--	0.86
Geometric mean					0.50

Table 2. Estimated number of walleye recruited at age 1 based on a residual index of relative year-class strength 1975-82.

Year class	Year-class strength	Multiplication factor ^a	Number at age 1 ^b
1975	0.65	1.2200	16,829
1976	0.13	0.6662	9,992
1977	1.02	1.6187	24,280
1978	0.88	1.4083	21,124
1979	1.56	2.7815	41,723
1980	-0.86	0.2450	3,681
1981	-1.55	0.1227	1,841
1982	-2.90	0.0351	526
Mean			15,000
SD			14,025

^a Multiplication factor = $e(\text{year class strength estimate})$. Values of multiplication factors have been standardized to a mean of 1.0.

^b Number at age 1 = (multiplication factor) (mean number at age 1).

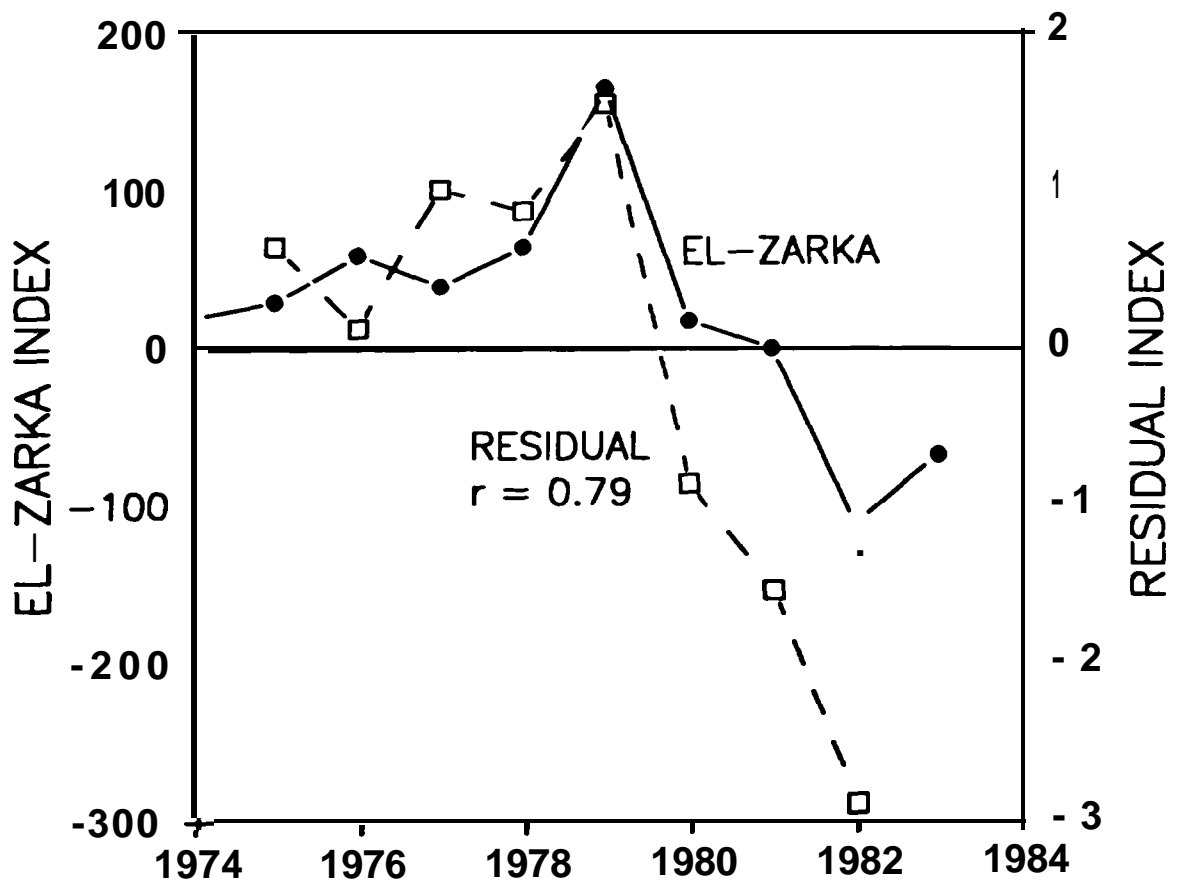


Figure 5. Indexes of relative year-class strength for walleye in John Day Reservoir estimated by a modified El-Zarka (1959) and a residual method.

(Figure 6). The maximum annual predation within the 100 year simulation was 520% higher than mean predation estimated for 1982. Maximum annual predation was 2,332% higher than the minimum and the coefficient of variation for predation was 0.49.

Predation was moderately sensitive to changes in growth and mortality (Table 3). Predation varied directly with +25% adjustments of growth rate, but varied inversely in response to +25% adjustments of mortality rate.

No difference in predation was detected between size limits of 10 and 14 inches or between 15 and 18 inches at all exploitation rates simulated (Figure 7). Predation by walleye was relatively insensitive to increased size of harvest at lower rates of exploitation.

Smallmouth bass

Age and growth - Growth of smallmouth bass as depicted by von Bertalanffy models was higher in the upper than in the lower John Day Reservoir. Models of von Bertalanffy were $L_t = 448[1 - e^{-0.1176(t - 0.226)}]$ for the upper reservoir and $L_t = 559[1 - e^{-0.165(t - 0.084)}]$ for the lower reservoir. Length at age estimates for the pooled upper and lower populations were fit to a von Bertalanffy equation of $L_t = 517[1 - e^{-0.207(t - 0.093)}]$. Growth of smallmouth bass was in the upper range compared with growth in other populations of smallmouth bass in northern USA and southern Canada (Figure 9).

Mortality - Mortality estimates differed between the lower and upper reservoir and with the method used for estimation. Catch curves for smallmouth bass from the lower and upper reservoir had smooth descending limbs after age 3 (Figure 9). Estimates of total instantaneous mortality for smallmouth bass greater than 3 years old were higher for the lower reservoir than for the upper reservoir. Mortality rates from cohort analysis differed between the lower and upper reservoir and were variable among cohorts. The geometric mean was higher for the lower reservoir (0.72) (Table 4) than in the upper reservoir (0.40) (Table 5). Natural instantaneous mortality estimated from Pauly's model (Pauly 1980) was 0.31 for the lower reservoir and 0.45 for the upper reservoir. The estimates of exploitation rate from tag returns given by Beamesderfer et al. (1987) were 0.45 for the lower reservoir and 0.24 for the upper reservoir. The combined Pauly model and Beamesderfer et al. (1987) estimates equated to total instantaneous mortality rates of 0.91 for the lower reservoir and 0.72 for the upper reservoir.

Year-class strength - Our two indexes of year-class strength of smallmouth bass showed similar patterns across years in the lower and upper reservoir (Figure 10). Strong year classes were evident in 1977 and 1979, and a weak year class was evident in 1981 for both lower and upper reservoir.

To simplify analysis, we chose the upper reservoir estimates of year-class strength to calculate relative recruitment. Our estimates of minimum and maximum recruitment between 1976 and 1982 varied 5-fold (Table 6). The standard deviation of mean recruitment accounted for a coefficient of variation of 0.53.

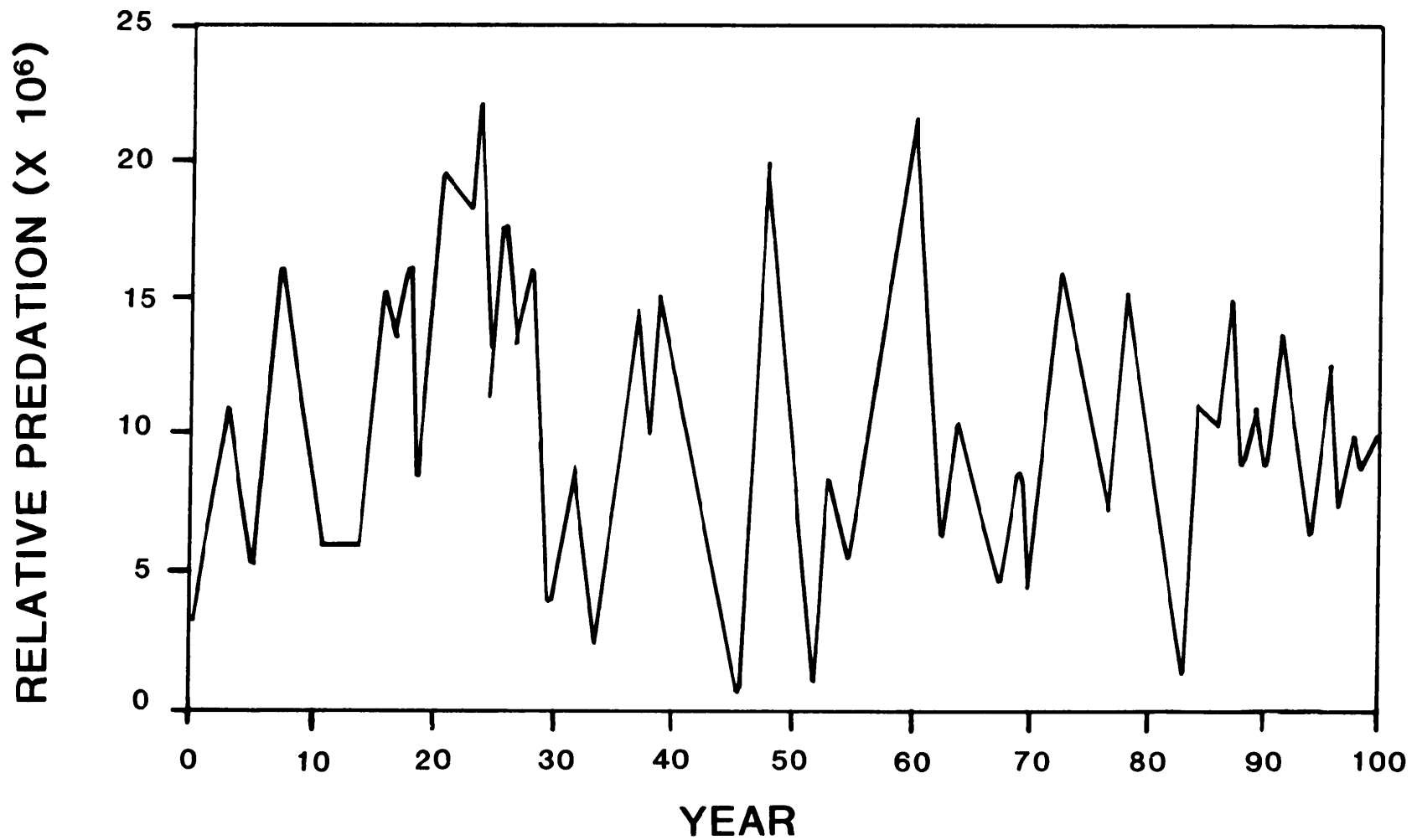


Figure 6. One-hundred-year simulation of potential predation of salmonid smolts by walleye in John Day Reservoir relative to predation in 1982.

Table 3. Sensitivity of mean relative predation and coefficient of variation of predation by walleye to variations in annual mortality and growth in 100-year simulations.

Parameter and adjustment	Percent change in mean relative predation ^a from best estimate	Coefficient of variation ^b
Growth rate (K):		
Best estimate (K = 0.335)	--	0.44
+25% (K = 0.419)	+ 37	0.51
-25% (K = 0.251)	- 40	0.36
Annual instantaneous mortality (Z):		
Best estimate (Z = 0.60)	--	0.44
+25% (Z = 0.75)	- 32	0.53
-25% (Z = 0.45)	+ 46	0.39

^a Mean relative predation = mean weighted effect of production + mean recruitment.

^b Coefficient of variation = mean weighted effect of production + SD of weighted effect of production.

Table 4. Age-specific catch and estimated mortality (total instantaneous) for five year classes of smallmouth bass in lower John Day Reservoir.

Year class	Catch at age							Mortality
	3	4	5	6	7	8	9	
1977	--	--	--		76	180	23	0.60
1978	--	--	--	89	63	14	--	0.92
1979	--	--	579	639	94	--	--	0.91
1980	--	257	149	43	--	--	--	0.89
1981	78	112	34	--	--	--	--	0.42
Geometric mean								0.72

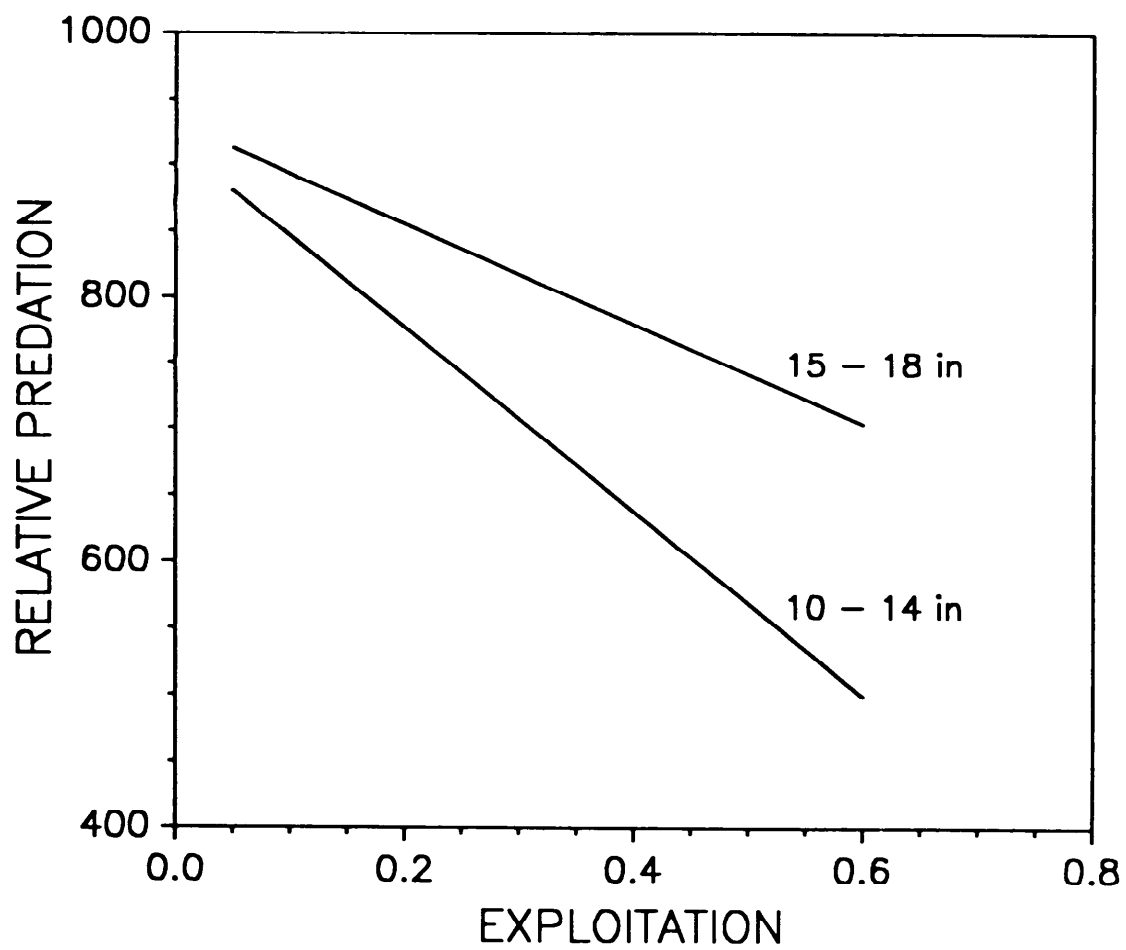


Figure 7. Variation of relative predation by walleye at differing rates of exploitation and minimum size at harvest.

Table 5. Age-specific catch and estimated mortality (total instantaneous) for five year classes of smallmouth bass in upper John Day Reservoir.

Year class	Catch at age							Mortality
	3	4	5	6	7	8	9	
1977	--	--	--	--	61	61	34	0.29
1978	--	--	--	27	6	14	--	0.33
1979	--	--	112	95	44	--	--	0.47
1980	--	231	106	48	--	--	--	0.79
1981	103	33	56	--	--	--	--	0.30
Geometric mean								0.40

Table 6. Estimated number of smallmouth bass recruited at age 1 in John Day Reservoir based on residual index of relative year-class strength for upper John Day Reservoir 1976-82.

Year class	Year-class strength	Multiplication factor ^a	Number at age 1 ^b
1976	0.16	0.9832	34,410
1977	0.66	1.6218	56,762
1978	-0.82	0.3697	12,941
1979	0.33	1.1680	40,881
1980	0.08	0.4075	31,763
1981	-0.99	0.3109	10,882
1982	0.67	1.6386	57,350
Mean			35,000
SD			18,650

^a Multiplication factor = $e(\text{year class strength estimate})$. Values of multiplication factors have been standardized to a mean of 1.0.

^b Number at age 1 = (multiplication factor) (mean number at age 1).

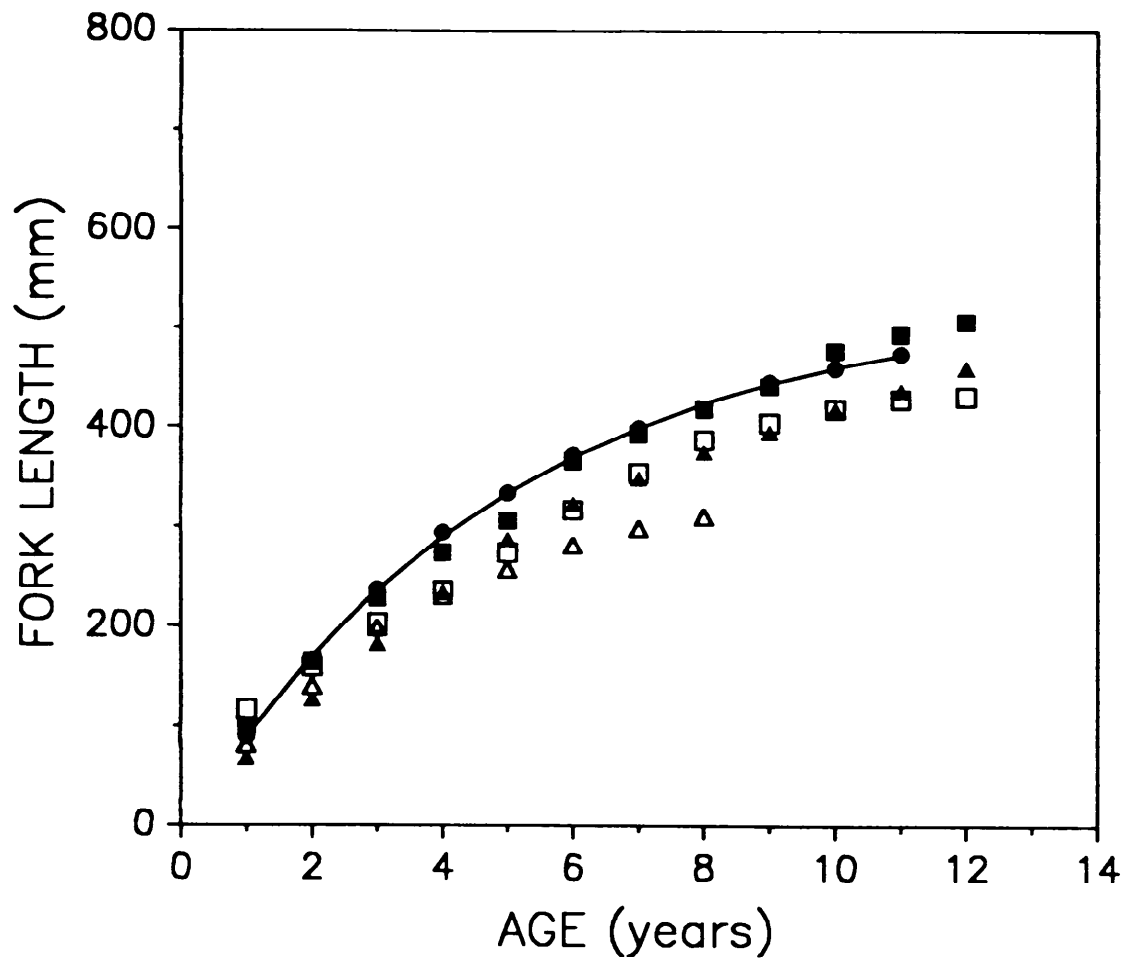


Figure 8. Comparison of growth for smallmouth bass in John Day Reservoir (●), combined lower and upper reservoir samples, to smallmouth bass from other waters in North America: Lower Snake River (▲) (Bennett et al. 1983); Middle Snake River (△) (Keating 1970); Great Lakes (□) (Carlander 1977); and Lake Simcoe, Ontario (■) (Robbins and MacCrimmon 1977).

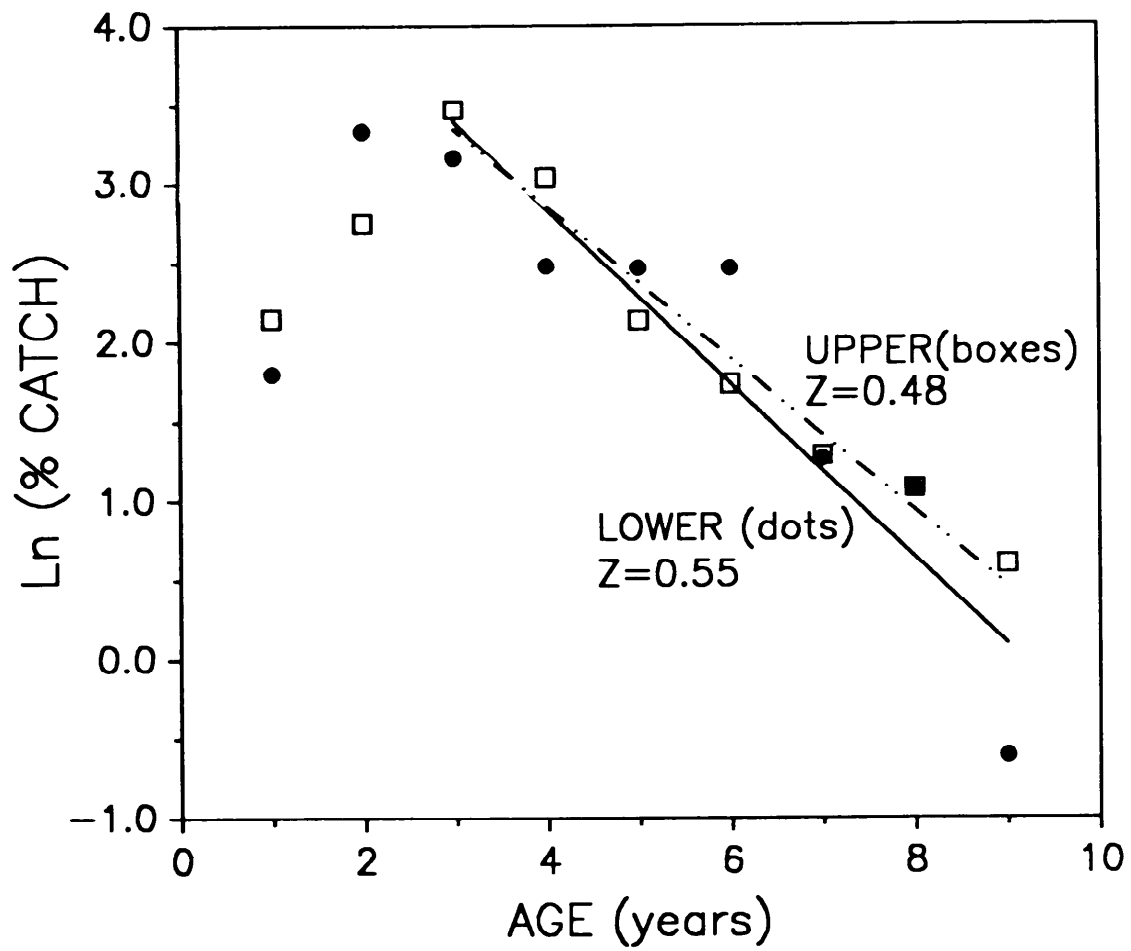


Figure 9. Catch curves for smallmouth bass in lower and upper John Day Reservoir from pooled data taken in 1983-86. Annual instantaneous mortality (Z) was estimated from a regression line of data for age 3-9 smallmouth bass.

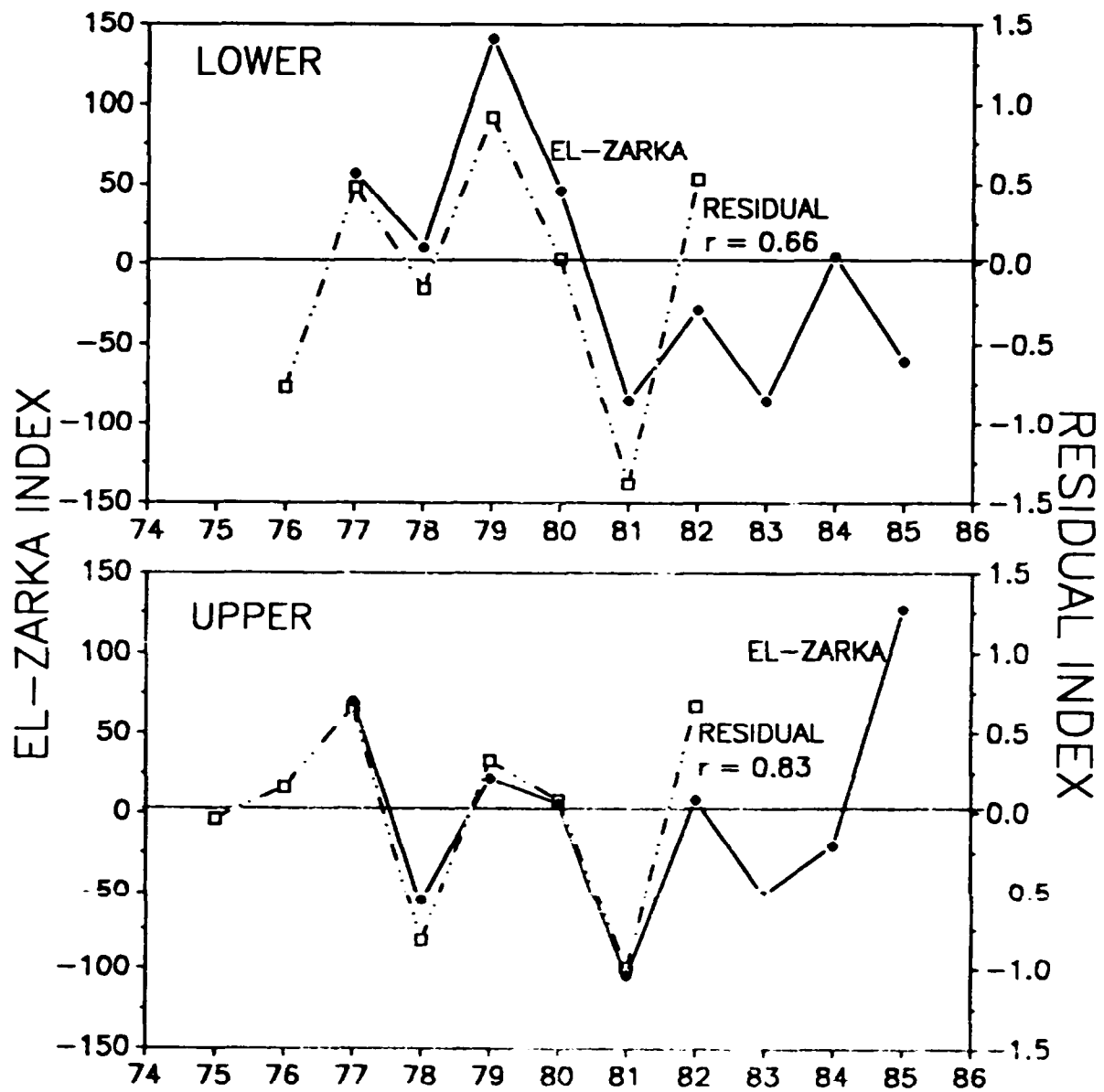


Figure 10. Indexes of relative year-class strength for smallmouth bass in lower and upper John Day Reservoir estimated by a modified El-Zarka (1959) and a regression method.

Indexes of year-class strength for smallmouth bass in the lower and upper reservoir were not consistently correlated with any physical variable (Appendix Tables 2 and 3). Length obtained at age 1 was consistently correlated with the El-Zarka (1959) index and the residual index of year-class strength ($r = 0.57$; 0.65 , respectively) in the upper reservoir, but not in the lower reservoir ($r = 0.14$; 0.54 , respectively).

Simulations of predation - Predation averaged 19% higher in a 100-year simulation than that estimated for 1982 (Figure 11). The maximum annual predation was 579% higher than the minimum annual predation within the 100-year simulation and was 105% higher than the mean predation estimated for 1982. The coefficient of variation in predation for the 100 year simulation was 0.28.

We found some sensitivity of predation to changes in growth and mortality (Table 7). Predation varied directly with $\pm 25\%$ adjustments in growth rate, but varied inversely with $\pm 25\%$ adjustments in mortality rate.

Predation by smallmouth bass decreased with increased exploitation. We found that predation was relatively sensitive to increased exploitation at 7 and 10 inches size at harvest, but relatively insensitive at 12 inches size at harvest (Figure 12).

Discussion

Strong compensation by walleye or smallmouth bass populations is not likely. We found that walleye grew well and Beamesderfer and Rieman (1988a) reported low densities (<1 per hectare) of walleye in John Day Reservoir. We believe then that the growth was not limited by density dependent factors. We would not expect a strong increase in growth with a reduced walleye population. A strong decrease in growth should not be expected until occurrence of much higher walleye abundance (Anthony and Jorgensen 1977) or radical habitat changes such as persistent colder temperature during the growth season (Carlander 1944) or decrease in food supply (Hokanson 1977).

Smallmouth bass grew well in John Day Reservoir. We have no explanation for the better growth of smallmouth bass in the upper reservoir compared with growth in the lower reservoir. It may be related to the quality of habitat offered by John Day River, a large tributary that enters at the lower reservoir. Also, the upper reservoir supported a lower density of smallmouth bass (Beamesderfer et al. 1987). Densities of smallmouth bass reported by Beamesderfer et al. (1987) for the upper and lower reservoir (<2 per hectare), however, appear too low to expect significant compensation of growth in these areas. Growth could vary with population abundance, but influence of temperature or unknown physical or biological factors should be more important at low densities (Rieman 1987).

Our direct estimates of mortality for walleye were variable and uncertain. The catch curve and cohort methods are both vulnerable to aging errors and bias. Variable year-class size and recruitment to sampling gear made estimates for walleye under age 6 unrealistic by either method. Variation among year classes also made the catch curve estimate for fish 6 years and older speculative. The Pauly model (Pauly 1980) estimate of natural

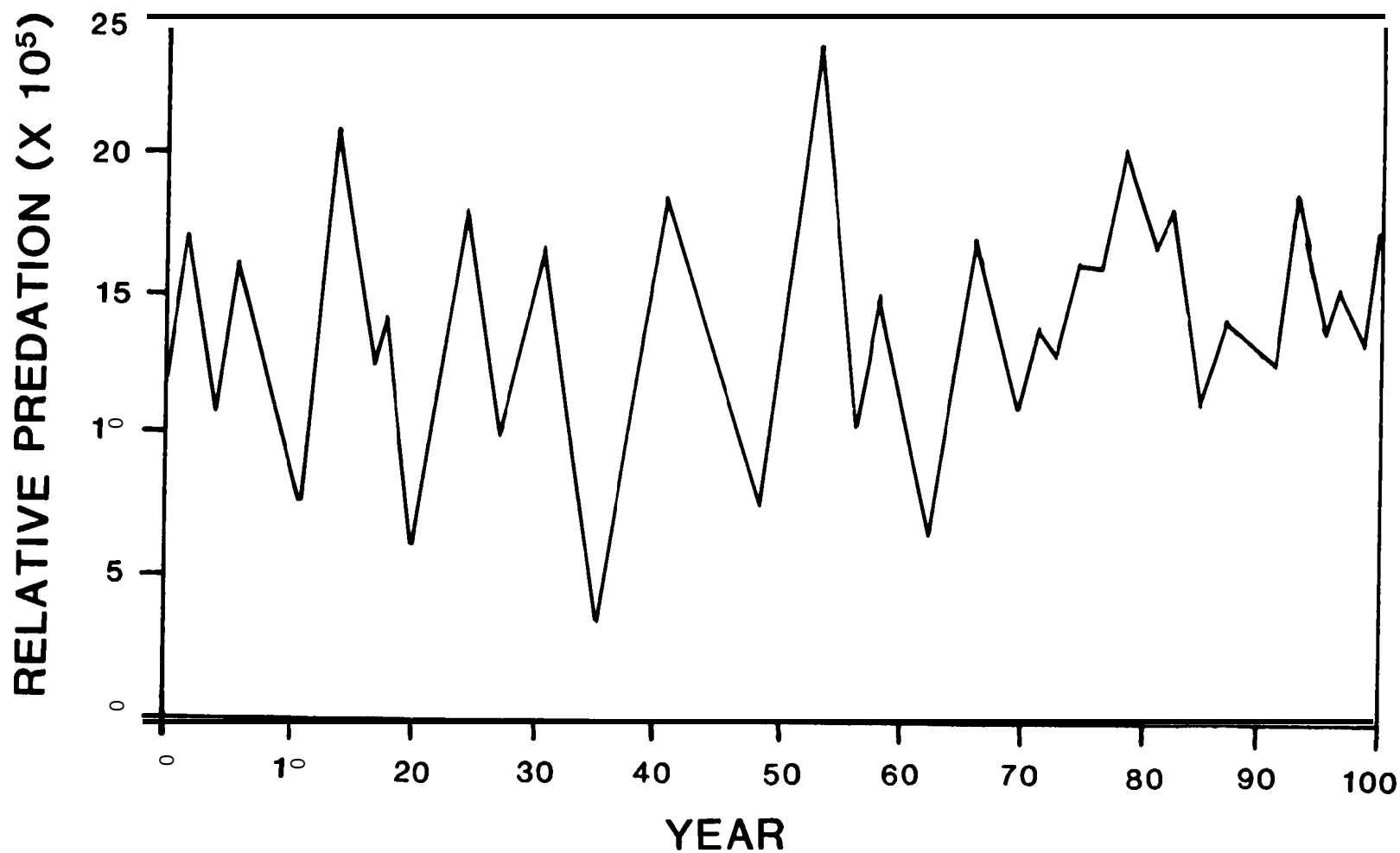


Figure 11. One-hundred-year simulation of potential predation of salmonid smolts by smallmouth bass in John Day Reservoir relative to predation in 1982.

Table 7. Sensitivity of mean relative predation and coefficient of variation of mean predation by smallmouth bass to variations in annual mortality and growth in 100-year simulations.

Parameter and adjustment	Percent change in mean relative predation^a from best estimate	Coefficient of variation^b
Growth rate (K):		
Best estimate (K = 0.207)	--	0.28
+25% (K = 0.259)	+ 42	0.30
-25% (K = 0.155)	- 32	0.24
Annual instantaneous mortality (Z):		
Best estimate (Z = 0.50)	--	0.28
+25% (Z = 0.625)	- 34	0.26
-25% (Z = 0.375)	+ 44	0.24

^a *Mean relative predation = mean weighted effect of production + mean recruitment.*

^b *Coefficient of variation = mean weighted effect of production + SD of weighted effect of production.*

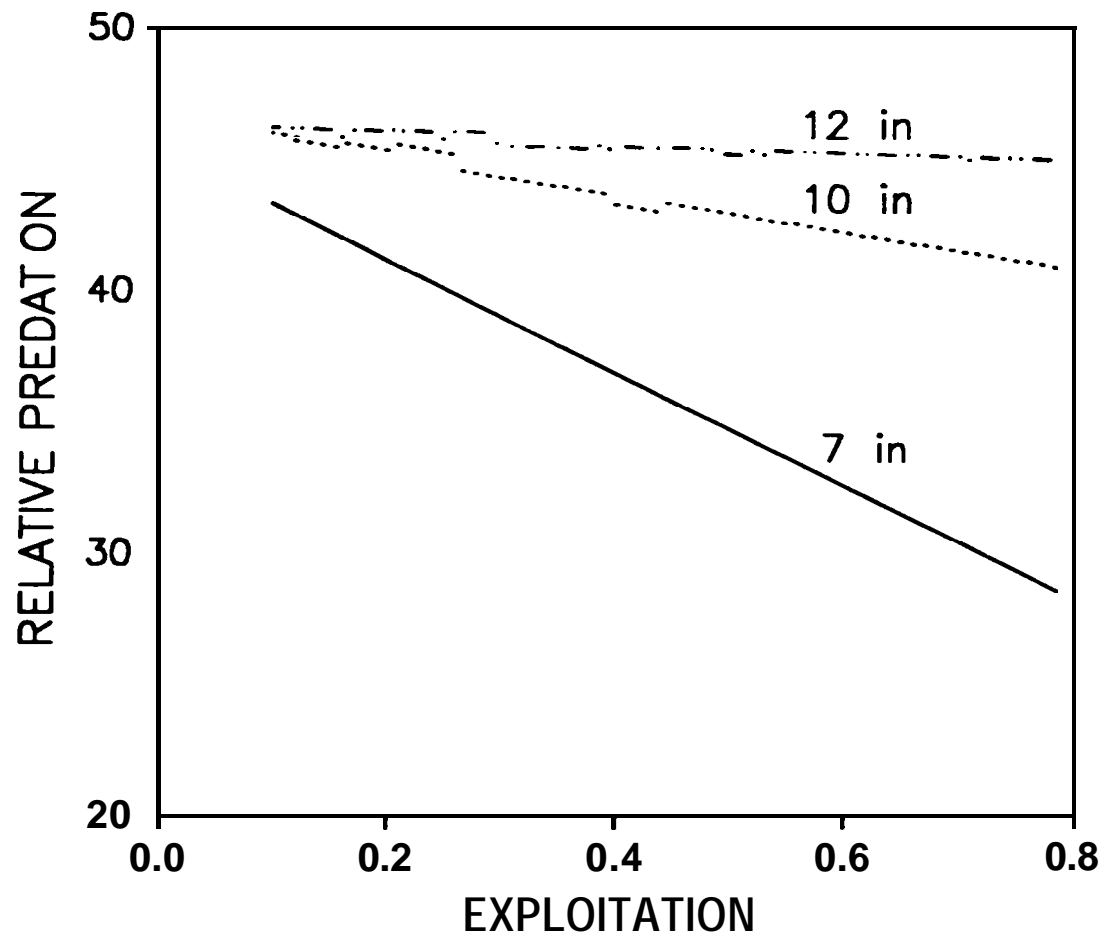


Figure 12. Variation of relative predation by smallmouth bass at differing rates of exploitation and minimum size at harvest.

mortality (0.45) was similar to values estimated in other walleye populations (Colby et al. 1979). Although this empirical model is indirect and was not developed for percids, it does appear to make reasonable predictions across broad taxonomic boundaries (Pauly 1980). When the recent exploitation estimate of 0.05 (Beamesderfer et al. 1987) was included, the estimate of total mortality (0.50) and the mean cohort estimate limited to fish older than 6 years (0.50) were considered estimates of current mortality. The catch curve estimate (0.72) was higher, but probably reflects historic rather than current mortality (Ricker (1975). Walleye fishing and fishing pressure has declined recently on John Day Reservoir. Fishing pressure was heavy in the early 1980s with the presence of the strong 1979 year class (R-C. Beamesderfer, Oregon Department of Fish and Wildlife, Research and Development Section, personal communication). As that year class declined, so did fishing pressure and probably exploitation. We believe the catch curve estimate of mortality better reflects mortality experienced by strong year classes. For the purposes of our simulations and year-class strength analyses we selected a central value of 0.60 as the best approximation of average mortality. For lack of better information we assumed mortality was constant with age after age 1.

Our estimates of mortality for smallmouth bass varied with method of estimation. Estimates from the cohort method were variable among cohorts with estimates for the lower and upper reservoir (0.72 and 0.40, respectively) differing from estimates by the catch curve method (0.55 and 0.48, respectively). Estimates of total annual mortality based on Pauly's (1980) model and exploitation estimates from Beamesderfer et al. (1987) for the upper and lower reservoir were higher (0.92 and 0.72, respectively). The estimates of natural mortality from the empirical model (0.31 to 0.45) were high relative to estimates summarized for the species (0.10 to 0.40, mean = 0.25) by Rieman (1987). For these reasons we believe that a central value of 0.50 from the direct estimates represents our best approximation of total mortality in John Day Reservoir. We used that value for our simulations and year-class strength analysis, and, as with walleye, we assumed mortality to be constant with age after age 1.

We found year-class strength of walleye strongly and positively correlated with estimated length at age 1. We also found indexes of walleye year classes correlated with several physical variables representing flow, reservoir elevation, and water temperature. Environmental influences have been implied by others (Machniak 1975; Groen and Schroeder 1978). Our data suggest that strong year classes may be associated with years of lower flow and years of higher temperature. High flow or reservoir elevation have typically been associated with strong year classes in other populations (Machniak 1975), but water temperature has frequently been considered important to growth (Carlander 1944; Huh et al. 1976; Colby et al. 1979) and ultimately to better survival (Forney 1976; Toney and Coble 1979). We suspect that low flow years actually provided higher water temperature, better conditions for first year growth, and ultimately stronger year classes of walleye. Flow might also act directly through some influence on habitat, but we cannot suggest a mechanism consistent with other studies.

We found evidence that year-class strength of smallmouth bass is influenced by first year growth. A faster growth rate during the first year of life provide a higher energy reserve before winter (Oliver et al. 1979).

Larger age 0+ smallmouth bass can experience significantly higher survival over the winter (Christie and Regier 1973; Shuter et al. 1980). Temperature during the growing season can have a primary influence on growth experience during the first year of life (Fry and Watt 1957).

We did not find any strong correlations between year-class strength of smallmouth bass and any of the environmental variables. Environmental influences are documented in other studies. Moderate drops in temperature ($>2^{\circ}\text{C}$) during spawning have been shown to disrupt spawning behavior of smallmouth bass, and drops in temperature during incubation or early rearing can lead to desertion of nests by guardian males (Christie and Regier 1973). Desertion of nests can expose young bass to significantly higher mortality, which could account for variations in year-class strength (Shuter et al. 1980). Henderson and Foster (1957) documented the adverse effects of influxes of colder water during spawning attempts by smallmouth bass in mid-Columbia River sloughs. Montgomery et al. (1980) showed that the combination of high water in 1976 followed by low water in 1977 created entrapment pools in slough areas of the mid-Columbia River near Hanford that caused higher than normal mortality of juvenile and adult smallmouth bass. Although we could not find any variable strongly correlated with smallmouth bass year classes, some combination of physical influences is probably important.

Despite our uncertainty in predicting walleye and smallmouth bass year classes, we do know that substantial variation can take place. Our simulations show that the variation in year-class size can result in variation in predation. Predation by walleye with random recruitment varied 24 fold (coefficient of variation = 0.49) in our simulation and predation by smallmouth bass varied jr-fold (coefficient of variation = 0.28). These variations were simply a result of the strong and weak year classes moving through the population age structure. The lag between the formation of a strong year class and strong predation effect was relatively short (1 to 2 years) because both predators began consuming juvenile salmonids at age 1. The predation imposed by a strong year class was also short-lived because prey consumption and predator number declined quickly with age. Similar simulations for northern squawfish *Ptychocheilus oregonensis* suggest that increases in predation may lag several years behind the formation of a strong year class and persist for up to 15 years (Rieman and Beamesderfer 1988). Predation by smallmouth bass and walleye will vary more from one year to the next than predation by northern squawfish.

Our results also show that the total loss to predation by walleye and smallmouth bass can be more important than shown in recent predation estimates. Rieman et al. (1988) estimated that walleye and smallmouth bass accounted for 13% and 9%, respectively, of salmonid loss from 1983 to 1986. Our data show the predation by walleye in 1982 was about one third of the average expected given normal variation in recruitment. Predation by smallmouth bass in 1982 was near the expected mean. We could not estimate the relative predation after 1982 for either species because we did not have the data to extend the indexes of year-class strength. We conclude that given normal variation in recruitment of all predators, walleye might actually contribute closer to 30% of the total loss in predation over many years. The

net increase in total predation in John Day Reservoir as a result of tripling the predation by walleye could be on the order of 25%. The anticipated change is relatively small given other variation in predation that can occur (Beamesderfer et al. 1988; Rieman and Beamesderfer 1988).

Changes in size limits for walleye and smallmouth bass did not influence predation strongly at exploitation rates in the ranges reported by Beamesderfer et al. (1987). At an exploitation rate of 0.50 for walleye, a size limit change from 12 inches (i.e., the potential size harvested under absence of regulations) to between 15 and 18 inches could account for a 4% increase in smolt predation. At an exploitation rate of 0.25 for smallmouth bass, a size limit change from 10 inches to 12 inches could account for a 2% increase in smolt predation. Effect of increasing minimum size at harvest is minimal because most predation was caused by walleye and smallmouth bass too small to be harvested. Management to promote a different population structure for walleye and smallmouth bass should have little conflict with management for better smolt survival.

Management for increased recruitment of walleye by stocking, managing water levels, or enhancing habitat could increase predation. However, Rieman and Beamesderfer (1988) suggest that strong year classes of walleye may actually reduce recruitment (and ultimately predation) in the now important predator, northern squawfish.

Our sensitivity analysis suggests that radical differences in predation by walleye and smallmouth bass with changes in growth and mortality are not likely. But uncertainty does exist. Our data were limited and we could not consider compensation in growth, mortality, predation, and species interactions in response to likely changes in physical and biological factors. We do not anticipate walleye and smallmouth bass becoming much more important to the predator-prey system but any attempt to manage predation should be accompanied by studies to monitor compensation in population characteristics and species interactions.

We conclude that variation in recruitment of walleye and smallmouth bass will influence predation on salmonid smolts. The variation is probably related to environmental influences and could be predictable. Walleye and smallmouth bass can be more important smolt predators than suggested by recent estimates. Probable changes are small, however, when compared with the major predator, northern squawfish. Management of the recreational fisheries for walleye and smallmouth bass will not cause any important increase in smolt predation unless predator recruitment is increased substantially. Even if walleye recruitment is enhanced, a net benefit in smolt survival might result.

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References

- Anthony, D. D., and C. R. Jorgensen. 1977. Factors in the declining contributions of walleye (*Stizostedion vitreum vitreum*) to the fishery of Lake Nipissing, Ontario, 1960-1976. *Journal of the Fisheries Research Board of Canada* 34: 1703-1709.
- Beamesderfer, R. C. 1988. MDCPOP: A flexible simulator for analysis of age-structured populations and stock-related functions. In T. P. Poe and B. E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir. (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Beamesderfer, R. C., and B. E. Rieman. 1988a. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: Part III. Abundance and distribution of northern squawfish, walleye, and smallmouth bass. In T. P. Poe and B. E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir. (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Beamesderfer, R. C., and B. E. Rieman. 1988b. Size selectivity and bias in estimates of population parameters of smallmouth bass, walleye, and northern squawfish in John Day Reservoir. In T. P. Poe and B. E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir. (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Beamesderfer, R. C., B. E. Rieman, J. C. Elliott, A. A. Nigro, and D. L. Ward. 1987. Distribution, abundance, and population dynamics of northern squawfish, walleye, smallmouth bass, and channel catfish in John Day Reservoir, 1986. Annual Report (Contract DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Beamesderfer, R. C., B. E. Rieman, and S. Vigg. 1988. Simulation of predation by northern squawfish on juvenile salmonids in a mainstem Columbia River Reservoir. In T. P. Poe and B. E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir. (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Bennett, D. H., P. M. Bratovich, W. Knox, D. Palmer, and H. Hansel. 1983. Status of the warmwater fishery and the potential of improving warmwater fish habitat in the lower Snake reservoirs. Report (Contracts DACW68-79-C0057) to U. S. Army Corps of Engineers, Walla Walla, Washington.
- Busch, W. D. N., R. L. Scholl, and W. L. Hartman. 1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie, 1960-1970. *Journal of the Fisheries Research Board of Canada* 32: 1733-1744.

- Carlander, K. D. 1944. Age, growth, sexual maturity, and population fluctuations of the yellow pike-perch, *Stizostedion vitreum vitreum* (Mitchill), with reference to the commercial fisheries, Lake of the Woods, Minnesota. Transactions of the American Fisheries Society 73: 90-107.
- Carlander, K. D. 1977. Handbook of freshwater fishery biology, volume 2. Iowa State University Press, Ames.
- Carlander, K. D. and R. R. Whitney. 1961. Age and growth of walleye in Clear Lake, Iowa, 1935-57. Transactions of American Fisheries Society 90:130-138.
- Christie, W.J., and H.A. Regier. 1973. Temperature as a major factor influencing reproductive success of fish-two examples. Rapports et Proces-verbaux des Reunions, Conseil International pour l'Exploration de la Mer 164:208-218.
- Colby, P.J., R.E. McNicol, and R.A. Ryder. 1979. Synopsis of biological data on the walleye *Stizostedion vitreum vitreum* (Mitchill 1818). Food and Agriculture Organization of the United Nations Fisheries Synopsis 119.
- Edwards, E.A., G. Gebhart, and O.E. Maughan. 1983. Habitat suitability information: smallmouth bass. U.S. Fish and Wildlife Service FWS/OBS-82/10. 36.
- El-Zarka, S.E. 1959. Fluctuations in the population of yellow perch, *Perca flavescens* (Mitchill), in Saginaw Bay Lake Huron. U.S. Fish and Wildlife Service Fishery Bulletin 151, Volume 59.
- Forney, J.L. 1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966-73. Journal of the Fisheries Research Board of Canada 33: 783-792.
- Fry, F.E., and K.E.F. Watt. 1957. Yields of year classes of smallmouth bass hatched in the decade of 1940 in Manitoulin Island waters. Transactions of the American Fisheries Society 85:135-143.
- Gray, G.A., and 11 coauthors. 1984. Feeding activity, rate of consumption, daily ration and prey selection of major predators in John Day Reservoir. Annual Report (Contract DE-AI-84BP34796) to Bonneville Power Administration, Portland, Oregon.
- Gray, G.A., and D.W. Rondorf. 1986. Predation on juvenile salmonids in Columbia basin reservoirs. Pages 178-185 in G.E. Hall and M.J. Van Den Avyle, editors. Reservoir fisheries management: Strategies for the 80's. Reservoir Committee, American Fisheries Society Southern Division, Bethesda, Maryland.
- Groen, C.L., and T.A. Schroeder. 1978. Effects of water level management on walleye and other cool water fishes in Kansas reservoirs. American Fisheries Society Special Publication 11:278-283.

- Henderson, C., and R.F. Foster. 1957. Studies of smallmouth black bass (*Micropterus dolomieu*) in the Columbia River near Richland, Washington. Transactions of the American Fisheries Society 86:112-127.
- Hokanson, K.E. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. Journal of the Fisheries Research Board of Canada 34:1524-1550.
- Huh, H.T., H.E. Colbert, and D.A. Stuiber. 1976. Effects of temperature and light on growth of yellow perch and walleye using formulated feed. Transactions of the American Fisheries Society 2:254-258.
- Keating, J.F., Jr. 1970. Growth rates and food habits of smallmouth bass in the Snake, Clearwater, and Salmon rivers, Idaho, 1965-1967. Master's thesis. University of Idaho, Moscow.
- Kelso, J.R.M., and T.B. Bagenal. 1977. Percids in unperturbed ecosystems. Journal of the Fisheries Research Board of Canada 34:1959-1963.
- Kelso, J.R.M., and F.J. Ward. 1977. Unexploited percid populations of West Blue Lake, Manitoba, and their interactions. Journal of the Fisheries Research Board of Canada 34:1655-1669.
- Kennedy, W.A. 1949. Relationship of length, weight, and sexual maturity to age in three species of Lake Manitoba fish. Fisheries Research Board of Canada Bulletin 81.
- Koonce, J.F., T.B. Bagenal, R.F. Carline, K.E.F. Hokanson, and M. Nagier. 1977. Factors influencing year class strength of percids: A summary and a model of temperature effects. Journal of the Fisheries Research Board of Canada 34:1900-1909.
- LaBolle, L.D. 1984. Importance of the upper littoral zone as a rearing area for larval and juvenile fishes in a Columbia River impoundment. Master's thesis. Oregon State University, Corvallis.
- Latta, W.C. 1975. Dynamics of bass in large natural lakes. Pages 175-182 in R.H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, D.C.
- Machniak, K. 1975. The effects of hydroelectric development on the biology of northern fishes (reproduction and population dynamics) III. Yellow walleye *Stizostedion vitreum vitreum* (Mitchill). A literature review and bibliography. Canada Fisheries and Marine Service, Department of Environment, Technical Report 529.
- McMahon, T.E., J.W. Terrel, and P.C. Nelson. 1984. Habitat suitability information: walleye. U.S. Fish and Wildlife Service, FWS/OBS-82/10.56.
- Momot, W.T., J. Erickson, and F. Stevenson. 1977. Maintenance of a walleye, *Stizostedion vitreum vitreum*, fishery in a eutrophic reservoir. Journal of the Fisheries Research Board of Canada 34:1725-1733.

- Montgomery, J.C., D.H. Fickeisen, and C.D. Becker. 1980. Factors influencing smallmouth bass production in the Hanford area, Columbia River. *Northwest Science* 54:296-305.
- Nicholas, J.W., and D.G. Hankin. 1988. Chinook salmon populations in Oregon coastal river basins: Description of life histories and assessment of recent trends in run strengths. Oregon Department of Fish and Wildlife, Information Reports, Fish 88-1, Portland.
- Noble, R.C. 1986. Predator-prey interactions in reservoir communities. Pages 137-143 in G.E. Hall and M.J. Van Den Avyle, editors. *Reservoir fisheries management: Strategies for the 80's*. American Fisheries Society Southern Division, Reservoir Committee, Bethesda.
- Oliver, J.D., G.F. Holeton, and K.E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. *Transactions of the American Fisheries Society* 108:130-136.
- Oregon Department of Fish and Wildlife and Washington Department of Fisheries. 1987. Columbia River fish runs and fisheries, 1960-1986. Status Report, Portland.
- Paragamian, V.L. 1987. Production of smallmouth bass in the Maquoketa River, Iowa. *Journal of Freshwater Ecology* 4:141-148.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperatures in 175 fish stocks. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* 39:175-192.
- Ploskey, G.R., and R.M. Jenkins. 1982. Biomass model of reservoir fish and fish-food interactions with implications for management. *North American Journal of Fisheries Management* 2:105-121.
- Poe, T.P., and nine coauthors. 1987. Feeding activity, rate of consumption, daily ration, and prey selection of major predators in John Day Reservoir, 1986. Annual Report (Contract DI-AI79-82BP34796) to Bonneville Power Administration, Portland, Oregon.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191.
- Rieman, B.E. 1987. Fishing and population dynamics of largemouth bass in select northern Idaho lakes. Doctoral dissertation. University of Idaho, Moscow.
- Rieman, B.E., and R.C. Beamesderfer. 1988. Population dynamics of northern squawfish and potential predation on juvenile salmonids in John Day Reservoir. In T.P. Poe and B.E. Rieman, editors. *Predation by resident fish on juvenile salmonids in John Day Reservoir*. (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.

- Rieman, B.E., R.C. Beamesderfer, S. Vigg, and T.P. Poe. 1988. Predation on resident salmonids in a mainstem Columbia River reservoir: Part IV. Total loss and mortality of juvenile salmonids to northern squawfish, walleye, and smallmouth bass. In T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir. (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Robbins, W.H., and H.R. MacCrimmon. 1977. Vital statistics and migratory patterns of a potamodromous stock of smallmouth bass, *Micropterus dolomieu*. Journal of the Fisheries Research Board of Canada 34:142-147.
- Schoneman, D.E., R.T. Pressey, and C.O. Junge. 1961. Mortalities of downstream migrant salmon of McNary Dam. Transactions of the American Fisheries Society 90:58-72.
- Serns, S.L. 1982. Influence of various factors on density and growth of age-0 walleyes in Escanaba Lake, Wisconsin, 1958-1980. Transactions of the American Fisheries Society 111:299-306.
- Shuter, B.J., J.A. MacLean, F.E.J. Fry, and A.A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Transactions of the American Fisheries Society 109:1-34.
- Sims, C.W., and F.J. Osslander. 1981. Migrations of juvenile chinook salmon and steelhead trout in the Snake River from 1973 to 1979. Report (Contract number DACW68-78-C0038) to U.S. Army Corps of Engineers, Portland, Oregon.
- Smith, L.L., Jr. 1977. Walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) populations and fisheries of the Red Lakes, Minnesota, 1930-75. Journal of the Fisheries Research Board of Canada 34:1774-1783.
- Taylor, M.W. 1981. A generalized inland fishery simulator for management biologists. North American Journal of Fisheries Management 1:60-72.
- Toneys, N.L., and D.W. Coble. 1979. Size-related first winter mortality of freshwater fishes. Transactions of the American Fisheries Society 108:415-419.
- U.S. Army Corps of Engineers. 1974, 1975,....1985. Annual fish passage report, Columbia and Snake rivers for salmon, steelhead and shad. North Pacific Division, Portland, Oregon.
- Vigg, S., T.P. Poe, L.A. Prendergast, and H.C. Hansel. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: Part II. Consumption rates, diel feeding chronology, and daily rations. In T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir. (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.

Walters, C.J. 1969. A generalized computer simulation model for fish population studies. Transactions of the American Fisheries Society 98:505-512.

Zar, J.H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Appendix Table 1. Spearman-rank correlation for year-class strength indexes for walleye and variables representing physical and biological conditions in John Day Reservoir.

Variable, time represented	Correlation coefficient (r)	
	El-Zarka index 1974-83	Residual index 1975-82
Walleye length^a:		
Age 1	0.85	0.90
Walleye year class strength:		
Previous year	0.65	0.46
Mean daily discharge^b:		
Jan- Dec	- 0.90	-0.71
Mar- May	-0.75	-0.36
May- Jul	-0.85	-0.79
Jun- Aug	-0.83	-0.86
Mar	-0.73	-0.36
Apr	-0.68	-0.33
May	-0.80	-0.52
Jun	-0.78	-0.88
Jul	-0.83	-0.79
Aug	-0.72	-0.69
Mean reservoir elevation^b:		
Mar	0.70	0.64
Apr	-0.21	0.00
May	-0.25	-0.19
Jun	0.33	0.69
Jul	-0.15	0.00
Aug	-0.40	-0.32
Standard deviation of reservoir elevation^b:		
Mar	-0.22	-0.24
Apr	0.12	-0.24
May	0.02	0.07
Jun	0.48	0.74
Jul	-0.35	-0.50
Aug	0.14	-0.26
May- Jul	0.23	0.38

^a Data from Beamesderfer et al. (1987).

^b Data from U.S. Army Corps of Engineers (1974-1983).

Appendix Table 1. Continued.

Variable, time represented	Correlation coefficient (r)	
	El-Zarka index 1974-83	Residual index 1975-82
Mean daily temperature^b:		
Apr-May	0.12	-0.02
Jun-Aug	0.57	0.76
May	0.58	0.38
Jun	0.44	0.71
Jul	0.64	0.76
Aug	0.41	0.55
Standard deviation of mean daily temperature^b:		
Mar	0.53	0.12
Apr	0.19	0.05
May	-0.78	-0.48
Daily change in mean temperature^b:		
Mar	0.62	0.12
Apr	0.18	-0.14
May	-0.58	-0.10
Jun	0.43	0.29
Jul	-0.47	-0.10
Aug	-0.33	-0.30
Total degree days-spawning^b:		
Nov-Apr 15 (Winter before hatching)	-0.15	-0.21
Total degree days-first winter^b:		
Nov-Mar (Winter after hatching)	-0.48	-0.81

Appendix Table 2. Spearman-rank correlation for year-class strength indexes for smallmouth bass and variables representing physical and biological conditions in lower John Day Reservoir.

Variable, time represented	Correlation coefficient (r)	
	El-Zarka index 1977-85	Residual index 1976-82
Smallmouth bass length^a:		
Age 1	0.14	0.54
Mean daily discharge^b:		
Jan- Dec	-0.80	-0.36
Mar- May	-0.52	0.04
May- Jul	-0.48	-0.32
Jun- Aug	-0.63	-0.32
Mean reservoir elevation^b:		
May	-0.47	-0.18
Jun	-0.02	-0.21
Jul	-0.02	-0.32
Standard deviation of reservoir elevation^b:		
May- Jul	0.34	0.18
May	0.48	0.82
Jun	0.39	0.04
Jul	-0.20	-0.23
Mean daily temperature^b:		
Mar- May	-0.32	-0.29
Jun- Aug	0.27	0.64
Total degree days-first year^b:		
Nov-Mar (Winter after hatching)	0.00	-0.11

^a Data from Beamesderfer et al. (1987).

^b Data from US Army Corps of Engineers (1976-1985).

Appendix Table 3. Spearman-rank correlation for year-class strength indexes for smallmouth bass and variables representing physical and biological conditions in upper John Day Reservoir.

Variable, time represented	Correlation coefficient (r)	
	El-Zarka index 1977-85	Residual index 1975-82
Smallmouth bass length^a:		
Age 1	0.57	0.65
Mean daily discharge^b:		
Jan-Dec	-0.38	-0.02
Mar-May	-0.22	0.17
May-Jul	-0.57	0.02
Jun-Aug	-0.58	-0.02
Mean reservoir elevation^b:		
May	0.13	-0.02
Jun	-0.08	-0.19
Jul	-0.27	-0.48
Aug	-0.38	0.06
Standard deviation of reservoir elevation^b:		
May-Jul	-0.18	-0.05
May	0.18	0.36
Jun	0.23	-0.10
Jul	-0.47	0.05
Aug	-0.30	-0.40
Total degree days-first year^b:		
Nov-Mar (Winter after hatching)	-0.03	0.19

^a Data from Beamesderfer et al. (1987).

^b Data from U.S. Army Corps of Engineers (1975-1985).

Appendix Table 4. Parameter estimates used in population simulation model^a.

Parameter	Parameter estimate		Source
	Walleye	Smallmouth bass	
von Bertalanffy coefficients:			
L _∞	715	517	Present study
K	0.335	0.207	
t ₀	-0.143	0.093	
Length-weight equation:			
Intercept	0.0000053	0.0000114	Oregon Department of Fish and Wildlife, Research and Development Section, Clackamas, unpublished data
Slope	3.13	3.07	
Recruitment:			
Mean	15,000	35,000	Present study
SD	14,025	18,650	
Total mortality:			
Conditional (A)	0.45	0.39	Present study
Instantaneous (Z)	0.60	0.50	

^a The model used was MOCPOP described by Beamesderfer (1988).

Appendix Table 5. Consumption function used in simulations of size-specific predation of salmonid smolts by walleye.

Fork length (mm)	Ration ^a estimate (mg smolts/g predator/day)	Conversion efficiency ^b (mg/g/day)	Consumption function ^c
<55	0	0	0
205	11.550	1.333	0.878
364	2.757	0.573	0.878
467	0.311	0.139	0.878
532	1.621	1.042	0.878
578	0.379	0.344	0.878
614	1.553	1.211	0.878
642	0.543	1.501	0.878
662	0.102	0.133	0.133
>683	0	0	0

^a Ration estimate from Vigg et al. (1988).

^b Conversion efficiency = Ration / 1,000 ($e^{G/153} - 1$), where $G = \ln wt_{agei+1} - \ln wt_{agei}$ and $wt = (5.3 \times 10^{-6}) + 3.13 FL$.

^c Mean conversion efficiency of 0.878 for fork lengths 205-642 mm was used to smooth the consumption function (see Figure 1).

Appendix Table 6. Consumption function used in simulations of size-specific predation of salmonid smolts by smallmouth bass.

Fork length (mm)	Ration ^a estimate (mg smolts/g predator/day)	Conversion efficiency ^b (mg/g/day)	Consumption function ^c
< 23	0	0	0
23-87	0.377	0.042	0.042
87-165	1.483	0.228	0.228
165-234	2.018	0.429	0.429
234-290	0.323	0.106	0.135
290-334	0.131	0.057	0.080
334-370	0.13	0.083	0.040
370-398	0	0	0.015
398-421	0	0	0
>421	0	0	0

^a Ration estimate from Vigg et al. (1988).

^b Conversion efficiency = $\text{Ration} / 1,000 (e^{G/153} - 1)$, where $G = \ln \text{wt}_{\text{age}i+1} - \ln \text{wt}_{\text{age}i}$ and $\text{wt} = (1.14 \times 10^{-5}) + 3.07 \text{ FL}$.

^c Conversion efficiency values for fork lengths 234-370 mm was hand fit with a regression line (see Figure 2) to smooth the consumption function.

Simulation of Predation by a Resident Fish on Juvenile Salmonids
in a Columbia River Reservoir

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Abstract.- We constructed a model of predation by northern squawfish *Ptychocheilus oregonensis* on juvenile salmonids migrating through John Day Reservoir. The model predicts mortality as a function of numbers of predators, distribution of predators, number of prey entering the reservoir, residence time of prey, water temperature, and flow. The model predicted mortality similar to that estimated from 1983-86, and also approximated differences among areas and months. Uncertainty analyses show predation mortality may vary threefold with normal annual variation in predator number, temperature, and flow. Mortality in 1983-86 was similar to the average predicted from 30 years of historic environmental data. Sensitivity analyses imply the best avenues for reducing predation are to reduce the number of predators, to pass salmonids earlier in the year, and to maintain runs of juvenile salmonids no less than present levels. Mortality, under the assumptions of the model, is little affected by changes in predator distribution, changes in consumption rate near the upstream dam, increases in number of prey, and decreases in residence time corresponding to increases in flow.

Production of salmon *Oncorhynchus* spp. and steelhead *Salmo gairdneri* in the Columbia River system is drastically reduced by mortality during outmigration (Ebel 1977). Predation by resident fish species accounts for much of the previously unexplained mortality in John Day Reservoir (Rieman et al. 1988). Predation mortality is dynamic, varying in time and space. A variety of factors that contribute to this variation have been identified. These include characteristics of the predator population such as species, number, size, and distribution; characteristics of the salmonid prey such as species, number, size, and behavior; and environmental characteristics such as temperature (Poe et al. 1988; Rieman et al. 1988; Vigg 1988; Vigg et al. 1988). Flow and residence time (Raymond 1979) are also suspected of affecting mortality but have not been related directly to predation.

Knowledge of the dynamics of predation can be useful to management. A better understanding may provide a predictive power useful in planning. Expected changes in predation over time with normal variation in the system could be described to determine whether recent mortality estimates (Rieman et al. 1988) are representative of what might be expected over a long term. In addition, if we know what factors affect mortality, we'll know what factors we might manipulate to increase salmonid survival and production. If we can quantify the functional relationships between driving factors and mortality, we can also evaluate alternative strategies.

Systems analysis methods provide a means of organizing and extracting information from our understanding of predation (Lackey 1975; Overton 1977). We constructed a model of the predator-prey system in John Day Reservoir. We used the model to organize our understanding of processes that regulate mortality of salmonids, to predict changes in predation over time with normal variation of the regulating factors, and to evaluate alternative strategies for reducing predation.

Methods

The factors incorporated into our mathematical model (Beamesderfer 1988) included predator number, predator distribution, prey number, timing of prey passage, prey residence time, water temperature, and water flow (cfs) through the reservoir. To simplify analyses, we treated factors that affect predation directly. Factors that indirectly affect predation by regulating predator population size and size structure were treated in a separate paper (Rieman and Beamesderfer 1988). We dealt only with northern squawfish *Ptychocheilus oregonensis* because they account for the majority (78%) of the predation (Rieman et al. 1988).

Parameters for the model were estimated to reflect the average condition in John Day Reservoir from 1983 through 1986 and yield mortality estimates similar to those reported for that period (Rieman et al. 1988). Model predictions were compared with empirical estimates to test the accuracy of the model.

We described the variation in mortality related to normal annual variation in the system by stochastically varying predator numbers, temperature, and flow for 30 years (uncertainty analysis). Predator numbers were varied to reflect changes resulting from observed variation in recruitment of northern squawfish (Rieman and Beamesderfer 1988). Environmental conditions were varied according to observed conditions for 30 years prior to 1987 (U.S. Army Corps of Engineers 1957-1986). Flow and temperature data for each year were used together to incorporate any covariation. We calculated approximate 95% confidence intervals for the long-term variation in predation as plus and minus two times the standard deviations observed in our 30-year simulation.

We ran a series of 1-year simulations in which various input parameters and initial state variables were adjusted by +1%, +10%, and +50% to evaluate the sensitivity of the model to these changes. We also plotted mortality versus a wide range of initial state variables (Table 1) and input parameters (Table 2) to examine the nature of the response in more detail. Sensitivity analysis was used to identify promising strategies for reducing predation mortality under the assumed set of conditions and relations defined in the model. We assumed the most promising strategies were those that manipulated conditions to which the model was sensitive.

Model Description

The model consists of a system of difference equations solved at daily intervals for a 150-day period that corresponds to the April through August period of salmonid outmigration. We used difference rather than differential equations because we felt diel variation in the system made solution for time intervals of less than 1 day unrealistic.

In the model, John Day Reservoir was divided into two areas: the tailrace immediately below McNary Dam at the upper end of the reservoir (the boat-restricted-zone, or BRZ), and the remaining body of the reservoir (Figure 1). This division follows differences in predation reported by Rieman et al. (1988). Predators in each area were apportioned from an entire-reservoir population according to time of the year (Table 1, Equations 2 and 5) to mirror seasonal changes in distribution reported by Beamesderfer and Rieman (1988). Number of predators in the BRZ could be scaled in response to number of prey to simulate the effects of a hypothetical numerical response (Table 1, Equations 3 and 4) (Krebs 1985). In addition, the reservoir-wide predator population was reduced throughout the season by a daily rate of mortality (Table 1, Equation 1). The model provided the option to apportion number of predators between active and inactive compartments (Table 1, Equation 6). We used the inactive compartment to simulate inhibition of predation during spawning (Vigg et al. 1988) or by high flow (Faler et al. 1988).

Prey were input at McNary Dam and passed through each area in sequence (Figure 2). We used a continuous function to generate daily

Table 1. Definitions of state and driving variables included in a model of predation in John Day Reservoir. p_1, \dots, p_{24} are parameters defined in Table 2.

Variable	Definition	Equation Number
$P_n(t)$	Number of predators in population at time t $= P_n(t-1) RD_m(t-1)$	1
$RD_m(t)$	Fraction of population that dies daily	
$P_{n1}(t)$	Number of predators in boat-restricted-zone $= P_n(t) RBrz(t)$	2
$RBrz(t)$	Fraction of predator population in BRZ $= p_1 + p_2 t + RNr(t)$	3
$RNr(t)$	Proportion to adjust distribution for prey number (to approximate numerical response) $= (-p_3 - p_4 (2p_3/(p_5 - p_4))) + (2p_3/(p_5 - p_4))$ $DJv(t)$	4
$P_{n2}(t)$	Number of predators in reservoir body $= P_n(t) - P_{n1}(t)$	5
$AP_{ni}(t)$	Number of predators in area i ($i = 1$ is BRZ, $i = 2$ is reservoir body) that are actively feeding $= P_{ni}(t) RAc_i(t)$	6
$RAc_i(t)$	Fraction of predator population in area i that is actively feeding.	
$Jv_1(t)$	Number of juvenile salmonids in BRZ ($= DJv(t)$)	
$DJv(t)$	Number of juvenile salmonids passing McNary Dam $= (p_6/(2.5066 p_7)) e^{-(p_8 - t)^{2/(2 p_7^2 - 2)}}$	7
$Jv_2(t)$	Number of juvenile salmonids in reservoir body $= Jv_2(t-1) - Jv_2(t-1)/RTmE(t-1) - SC_2(t-1)$ $+ DJv(t) - SC_1(t)$	8
$RTmE(t)$	Exponential residence time for prey in the reservoir $= RTm(t) / -Ln0.5$	9
$RTm(t)$	Average residence time (days) $= 1 / (p_9 + p_{10} DF_1(t))$ (optional)	10

Table 1. Continued.

Variable	Definition	Equation Number
DF1(t)	Flow rate (10^3 CFS) at dam $= p_{11} e^{-(p_{12} - t)^2 / (2 p_{13} \cdot 2)}$	11
SC1(t)	Number of prey consumed by predators in BRZ $= APn1(t) RCn1(t)$	12
RCn1(t)	Consumption rate of prey per predator in BRZ $= RCn_{max}(t) / (1 + p_{14} e^{-p_{15} Jv1(t)})$	13
RCn_{max}(t)	Maximum potential consumption rate (prey per predator per day) $= p_{16} DTp(t)^2 - p_{17} DTp(t)^3 + p_{18} DTp(t)^4 - p_{19} DTp(t)^5 + p_{20} DTp(t)^6$	14
DTp(t)	Temperature (degrees centigrade) in reservoir at time t $= p_{21} + p_{22} t$	15
SC2(t)	Number of prey consumed by predators in reservoir body $= APn2(t) RCn2(t)$	16
RCn2(t)	Consumption rate of prey per predator in reservoir body $= RCn_{max}(t) / (1 + p_{23} e^{-p_{24} Jv2(t)})$	17

Table 2. Definitions of parameters and values used in a model of predation in John Day Reservoir.

Reference equation number	Symbol of parameter	Description of parameter	Value of parameter
3	p1	Intercept for proportion in BRZ	0.0448
	p2	Slope for proportion in BRZ	3.13×10^{-4}
4	p3	Change in proportion (+) with specified range in passage number	0
	p4	Minimum daily passage	19,000 ^a 0 ^{bc}
	p5	Maximum daily passage	235,000 ^a 241,000 ^b 204,000 ^c
7	p6	Number of salmonids in run	2.10×10^7 ^a 1.17×10^7 ^b 9.39×10^6 ^c
	p7	Day of peak passage	70 ^a , 47 ^b , 99 ^c
	p8	Index of run duration (days in one standard deviation from day of peak passage)	36 ^a , 19 ^b , 18 ^c
10	p9	Intercept for residence time	0.076
	p10	Slope for residence time	0.0007
11	p11	Maximum discharge at McNary Dam	282
	p12	Day of maximum discharge	48
	p13	Days in one standard deviation from day of maximum discharge	64
13	p14	Constant referring to intercept for consumption rate in BRZ	12.4
	p15	Constant referring to response rate to increasing prey for consumption rate in BRZ	1.23×10^{-5}
14	p16	Coefficient for maximum potential consumption rate versus temperature	1.147×10^{-1}
	p17	Coefficient for maximum potential consumption rate versus temperature	3.019×10^{-2}
	p18	Coefficient for maximum potential consumption rate versus temperature	2.880×10^{-3}

^a Combined early and late runs of salmonids.

^b Early run of salmonids.

^c Late run of salmonids.

Table 2. Continued.

Reference equation number	Symbol of parameter	Description of parameter	Value of parameter
14	p19	Coefficient for maximum potential consumption rate versus temperature	1.110x10⁻⁴
	p20	Coefficient for maximum potential consumption rate versus temperature	1.476x10⁻⁶
15	p21	Intercept for temperature	8.74
	p22	Slope for temperature	0.108
17	p23	Constant referring to intercept for consumption rate in reservoir	23.5
	p24	Constant referring to response rate to increasing prey for consumption rate in reservoir	3.1x10⁻⁷

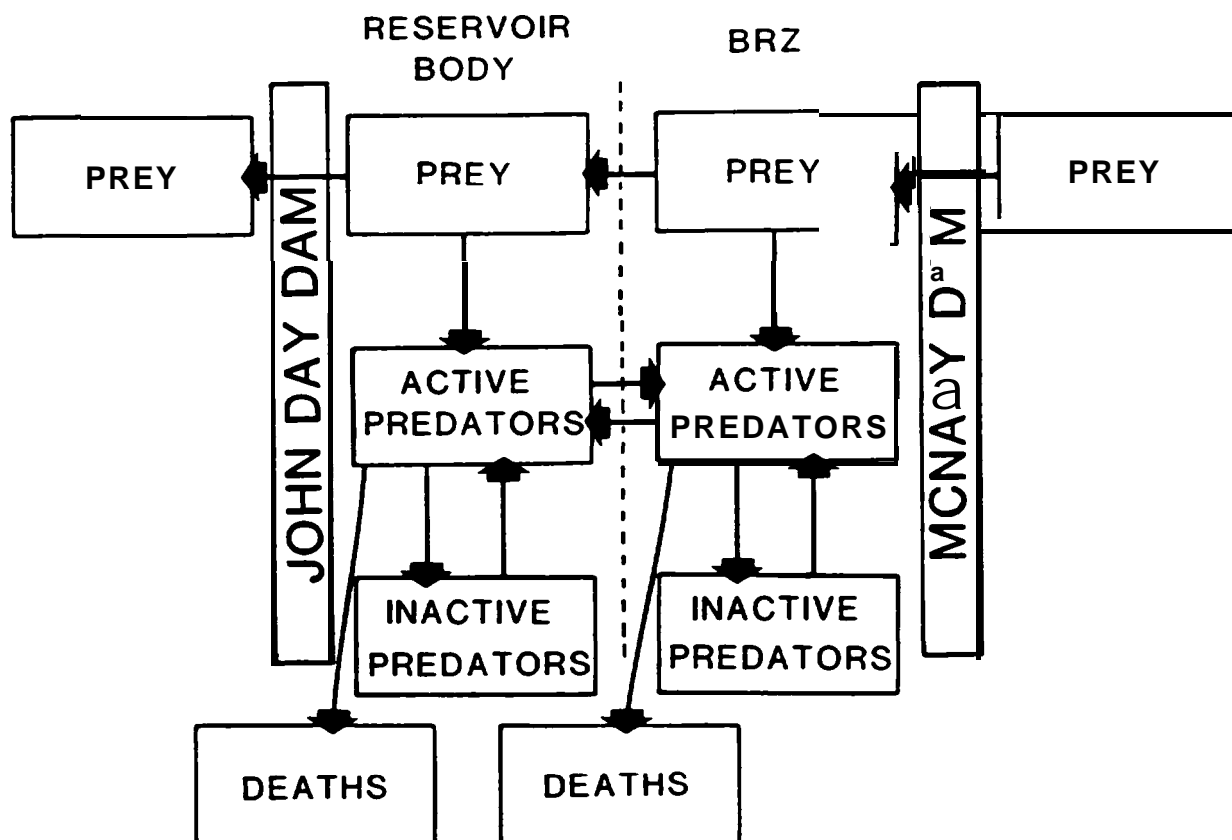
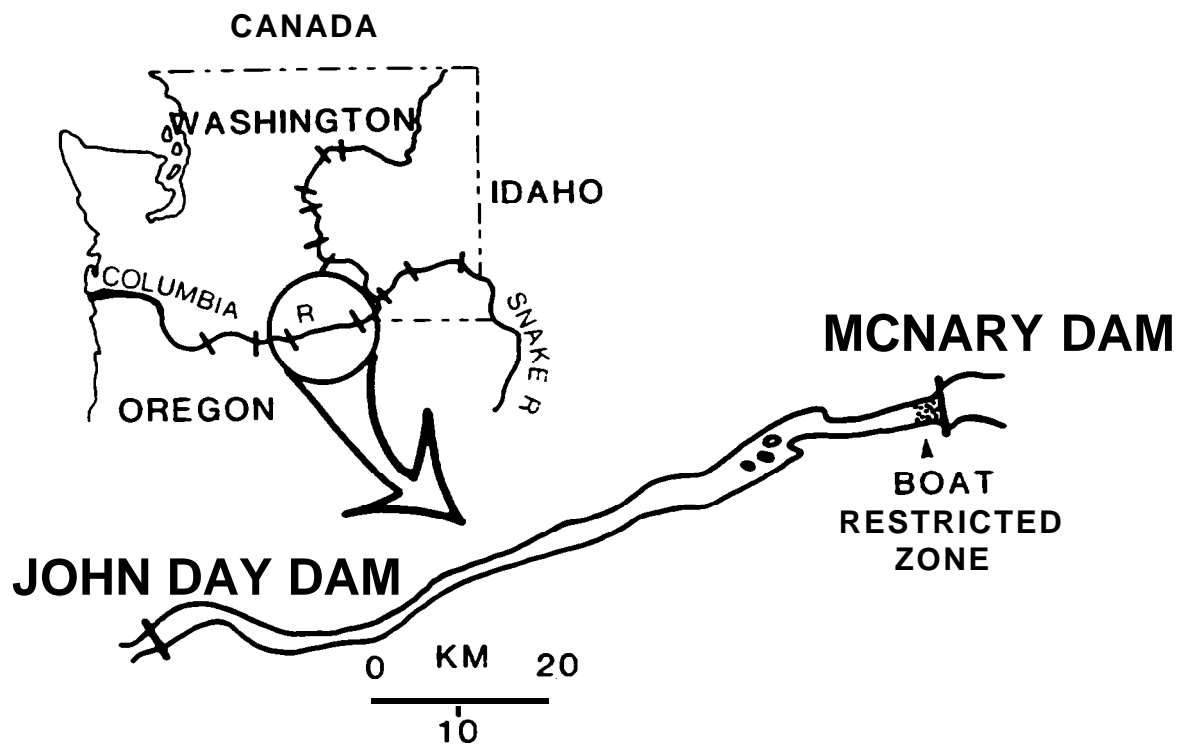


Figure 1. Conceptual model of predation by northern squawfish on juvenile salmonids in John Day Reservoir.

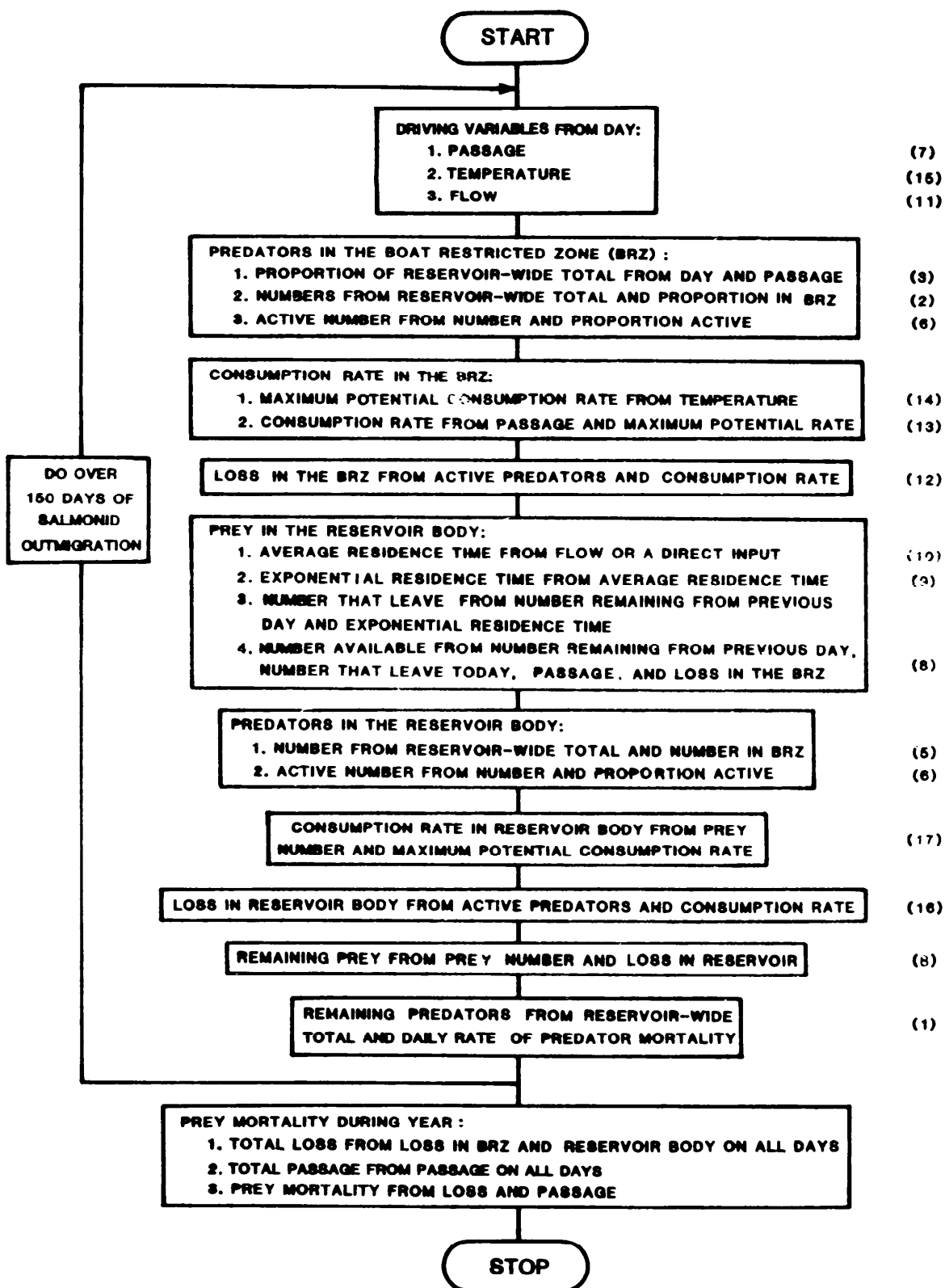


Figure 2. Sequence of calculations in model of predation in John Day Reservoir. Reference equation numbers from Table 1 are included in parentheses.

prey number. Giorgi and Sims (1987) described patterns of daily passage of steelhead and salmon, which resemble normal distributions. We therefore described prey passage at McNary Dam as a normal function of time (Table 1, Equation 7). The number of prey in the reservoir was regulated by input rates and residence times (Table 1, Equation 8). Inputs into the BRZ correspond to passage past McNary Dam. Residence time in the BRZ was ignored because the small area of the BRZ and the flushing action of high flows past McNary Dam probably resulted in residence time considerably shorter than one day. Particle residence time in the BRZ averages less than one hour. Because of high velocity in the BRZ (Faler et al. 1988), we believe salmonids do not have a residence time significantly different from that of particles.

Inputs of prey into the reservoir body include those salmonids that pass McNary Dam and survive predation in the BRZ. Residence time in the reservoir was represented as an exponential decay function in which some proportion of the prey population left the reservoir daily. Days when 50% of a cohort of prey remained corresponded to an average passage time (Table 1, Equation 9). Residence time could be input directly or could be described as an inverse linear function of flow. We used the model developed by Sims et al. (1984) to describe the residence time-flow relationship (Table 1, Equation 10). We used direct inputs of residence time except when evaluating the response of mortality to flow. Flow past McNary Dam was described as a normal function of time. The March through August period of our simulations includes the spring peak flow and the decline to summer low flow. We described the hydrograph as a normal distribution of flow with time (Table 1, Equation 11).

We modeled prey consumption rate (per predator) as a logistic function of prey number. The logistic model represents the Type III "functional response" exhibited by predators with increasing prey availability (Holling 1959; Peterman and Gatto 1978). Vigg (1988) described a logistic functional response to salmonid density for northern squawfish in the BRZ. We assumed a similar relationship existed in the body of the reservoir. Consumption rate was related to passage number in the BRZ (Table 1, Equation 13) and number of prey calculated from passage and residence time in the reservoir (Table 1, Equation 17). Vigg (1988) assumed that consumption rate in the BRZ was related to passage, temperature, and a flow-related residence time but failed to demonstrate a significant flow effect. We estimate inclusion of flow increases r^2 values in regressions of passage and temperature on consumption rate in the BRZ by only 2%. Predation in the BRZ was thus assumed to be a lie-in-wait process where predators had one chance to capture a salmonid as it passed. Predation in the reservoir was simulated as a rover-predator process where prey were continuously exposed to predators until they passed from system.

Beyer et al. (1988) showed that consumption rate of northern squawfish varies with temperature. We incorporated effects of seasonally changing temperature on consumption rate by describing maximum rate of consumption (asymtote in functional response, Table

1, Equations 13 and 17)) as a function of temperature. Vigg and Burley (1988) described the maximum consumption rate for northern squawfish as a polynomial function of temperature. We used the relationship of Vigg and Burley (1988) to modify our consumption model on a daily basis (Table 1, Equation 14). Temperature was described as a linear function of time (Table 1, Equation 15). Temperature increased steadily from March through August simultaneous to the decline in flow.

Loss was estimated each day in each area as the product of number of active predators and daily consumption rate (Table 1, Equations 12 and 16). Mortality was estimated by dividing total loss to predators in any period of time by number of salmonids entering the reservoir in that time period.

Parameter Estimation

Predators.— We used an average of the number of northern squawfish (85,000) estimated by Beamesderfer and Rieman (1988) for John Day Reservoir in 1984-86 as a starting predator number. The estimates include only fish 250 mm in length and larger. Northern squawfish smaller than 250 mm did not consume salmonids in significant numbers (Poe et al. 1988). Variance in number of predators was estimated for uncertainty analysis using the long-term variation in potential predation by northern squawfish predicted by Rieman and Beamesderfer (1988). Predicted variation was based on variation in year-class strength and population size structure that resulted from variation in recruitment over 15 years prior to 1986. For each year in our 30-year simulation, we randomly selected a predator number from a normal distribution, with mean and variance from Rieman and Beamesderfer (1988).

To estimate mortality of predators during the year, we assumed the sole source of mortality from April through August was exploitation. We used the average exploitation (0.02) estimated by Rieman and Beamesderfer (1988) for northern squawfish in 1984-86 to calculate a daily rate of mortality. We assumed

$$1 - E = (1 - RDm(t))^{150}$$

where

$$\begin{aligned} E &= \text{proportion of population removed by anglers} \\ &\quad \text{annually,} \\ &= 0.02. \end{aligned}$$

Hence,

$$RDm(t) = 1 - (1 - E)^{6.67 \times 10^{-3}} = 0.000135$$

We used a regression to estimate parameters (Table 2) in the function relating the proportion of northern squawfish in the BRZ with time ($r^2 = 0.19$). Monthly estimates of proportion were calculated from relative catch per unit effort in and out of the BRZ after Rieman et al. (1988). The estimated proportions were compared with dates corresponding to midpoints of months.

We apportioned fish into inactive compartments in June to show reduction in consumption rate during that period. Vigg (1988) speculated that reduced feeding by northern squawfish while spawning accounts for this decline and the lack of a functional response during June. Proportions were selected by calibration until desired reductions in loss were achieved. Resulting proportions of active fish were 0.20 in the BRZ and 0.24 in the reservoir.

We attempted to describe a numerical response of northern squawfish in the BRZ to salmonid number. We used catch per unit effort (CPUE) of electrofishers to estimate relative densities of predators in the BRZ (Beamesderfer and Rieman 1988). However, we found no significant correlation between CPUE and salmonid number ($r^2 = 0.044$). We therefore set the strength of the numerical response to zero.

Prey.— Average number and temporal distribution of salmonids that entered the reservoir was described using average daily passage by month for 1983-86 (Rieman et al. 1988). We related mean daily passage in each month to the day corresponding to the midpoint of the month. Normal curves (Figure 3A) were fit with nonlinear regressions. Three groups of salmonids were described: all stocks combined ($r^2 = 0.93$); an early run including steelhead, all salmon in April and May, and half of the salmon entering in June ($r^2 = 0.99$); and a late run including half the salmon entering in June and all salmon entering in July and August ($r^2 = 0.99$). We used inputs for all stocks combined to simulate mortality for comparisons with empirical estimates of mortality, in uncertainty analyses, and in analyses of model sensitivity to 1%, 10%, and 50% adjustments in inputs. We averaged sizes and durations of early and late runs when examining the effect of day of peak passage on mortality in the detailed sensitivity analysis. We used inputs for early and late runs separately to examine effects of changing the duration of passage of a stock.

Estimated residence time of salmonids in John Day Reservoir during March and May using an equation relating rate of downstream movement of steelhead between McNary and John Day Dams to river flow rate in 1982-83 (Sims et al. 1984). This equation is

$$Y = 9.35 + 0.09 X$$

where

Y = rate of movement (km/day), and

X = river flow at John Day Dam (10^3 cfs).

We solved the equation for days to travel through the 123-km reservoir to fit the form used in the model (Figure 3B). We calculated a mean travel time of 4 days for use in the model for early run fish by substituting in average flow during the March to June period of steelhead outmigration (269×10^3 cfs in 1984-86). We assumed travel time of spring chinook salmon in the early run was similar to that of steelhead because Sims et al. (1984) reported differences of less than 3% in average travel time from Lower Granite Dam to John Day Dam from 1973-83. For late-run fish, we used travel time of 22 days estimated from averages reported for fall chinook

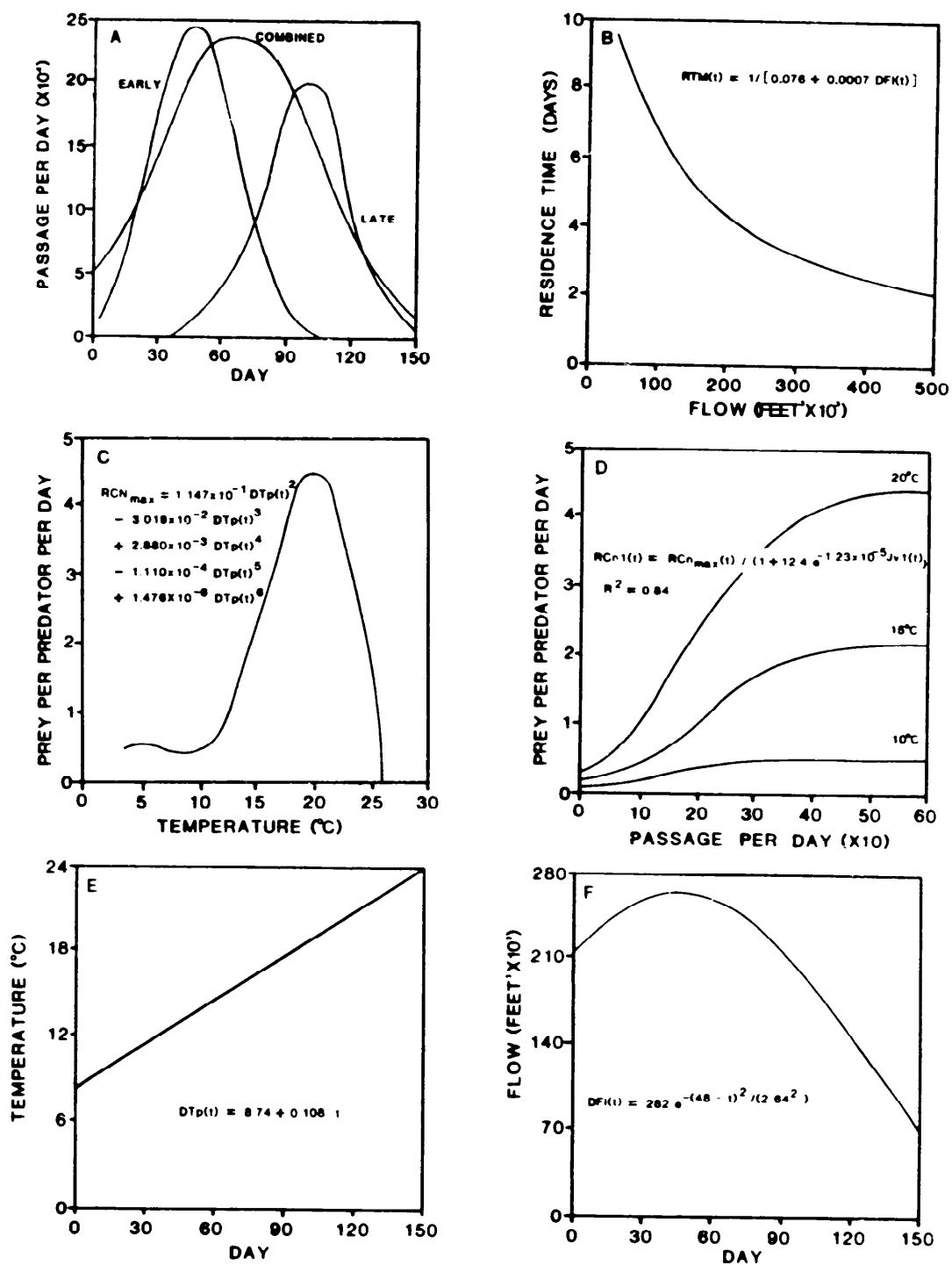


Figure 3. Relationships used in a model of predation by northern squawfish on juvenile salmonids into John Day Reservoir. (A) average daily passage of juvenile salmonids, April to August. (B) flow vs residence time of juvenile salmonids. (C) temperature vs maximum consumption of salmonid prey by northern squawfish (Vigg and Burley 1988). (D) consumption rates of northern squawfish in the boat-restricted zone at McNary Dam vs numbers of juvenile salmonids at three temperatures. (E) average daily temperature vs day. (F) flow vs day.

salmon through John Day Reservoir in 1981-83 (Miller and Sims 1984). We averaged early and late run travel times to represent the entire season.

We used parameters from the equation for steelhead to relate flow and travel time throughout the year although we recognized travel time of late run fish would be underestimated and no strong flow-travel time relationship is apparent for late-run fish (Miller and Sims 1984). Flow-travel time relationships are similar between steelhead and spring chinook salmon (Sims et al. 1982).

Consumption Function. - We used parameter estimates for the temperature and maximum-potential consumption function (Table 1, Equation 14) from Vigg and Burley (1988) (Figure 3C). We used nonlinear regressions to estimate remaining parameters for the functional response equation (Table 2). In the BRZ, we calculated a regression of maximum consumption and passage on observed consumption rate (Figure 3D). We estimated a maximum-potential consumption rate on 34 sample dates from 1984-86 by substituting temperature into the rate equation (Table 1, Equation 14). June was omitted because Vigg (1988) indicated that the functional response breaks down in June. Daily passage was estimated after Rieman et al. (1988). We fit remaining parameters in the functional response equation in the reservoir with a regression of maximum-potential consumption and number of available prey on observed consumption rate ($r^2 = 0.62$). Monthly means were used. Maximum potential consumption was calculated as in the BRZ. Consumption rates were from Vigg et al. (1988). Prey numbers were estimated with the model based on passage and residence time estimates (Table 1, Equation 8).

Temperature and Flow. - We used temperature data collected concurrent with sampling for predators to describe a temperature relationship with time. Regressions were used to fit data from April through August 1984-86 (average $r^2 = 0.74$). We represented average conditions during the three years by averaging slope and intercept parameters (Figure 3E). For the uncertainty analysis, we used lines fit to daily temperature data at McNary Dam from 1957 through 1986 (U.S. Army Corps of Engineers 1957-86). Coefficients of determination over the 30 years averaged 0.97.

Normal curves were fit to daily flow at McNary Dam (U.S. Army Corps of Engineers 1984, 1985, 1986) using a nonlinear regression (Figure 3F). A curve was fit to monthly mean flow for each year from 1983 through 1985 (average $r^2 = 0.99$), and parameters for each year were averaged (Table 2). We fit curves to daily flow at McNary Dam from 1957-86 (U.S. Army Corps of Engineers 1957-86) for use in the uncertainty analysis (average $r^2 = 0.98$).

Results

Simulation results generally corresponded with estimated losses and mortality to northern squawfish. The model predicted an annual loss of 2,500,000 prey and an annual mortality of 0.12. Rieman et al. (1988) estimated loss and mortality to northern squawfish at 2,300,000 and 0.11, respectively. The model also reflects observed differences in mortality between the BRZ and the reservoir body. The model calculated loss in the BRZ at 22% of the total while Rieman et al. (1988) estimated mortality at 28%. Seasonal patterns in loss and mortality predicted with the model were also similar to the estimates (Figure 4).

We estimated from model simulations that predation mortality may vary +44% from the mean based on normal annual variation in predator number, temperature and flow over a 30-year simulation. These bounds corresponded to approximate 95% confidence intervals. The model's prediction of mortality using parameter estimates for 1984-86 was 142 greater than the average estimated for the 30-year period.

Mortality of salmonids was most sensitive to changes in predator number at the start of the year, predator activity level, maximum-potential consumption rate, and the intercept parameter for the functional response in the body of the reservoir (Table 3). Changes in these parameters resulted in nearly proportional changes in mortality. Mortality was also moderately sensitive to changes in prey number, timing of prey passage, prey residence time, the rate parameter for the functional response in the reservoir body, and temperature equation parameters. Changes in these parameters resulted in relative changes in mortality of at least 10% of the change in the parameter. Mortality was relatively insensitive to changes in daily predator mortality, predator distribution between the BRZ and reservoir body, the duration of prey passage, the residence time-flow relationship, functional response parameters in the BRZ, and flow. Varying these parameters resulted in changes in mortality of 10% or less.

Changes in input parameters or starting conditions most commonly resulted in linear or nearly linear responses in predictions of prey mortality. For instance, mortality increased in direct proportion to increased predator number, fraction of predators in the BRZ, fraction of predators actively feeding, maximum consumption rate and response rate parameters in the functional response equation. Linear decreases in prey mortality were seen with increasing predator mortality.

Total mortality was a curvilinear function of residence time of prey, flow, and intercept parameter of the functional response. Increases in mortality with increased residence time resulted only within the body of the reservoir (Figure 5A). We assumed mortality in the BRZ was constant because predators there responded directly to passage rather than density determined by number entering and residence time. The relationship of residence time and mortality was also evident in an inverse relationship between flow and mortality

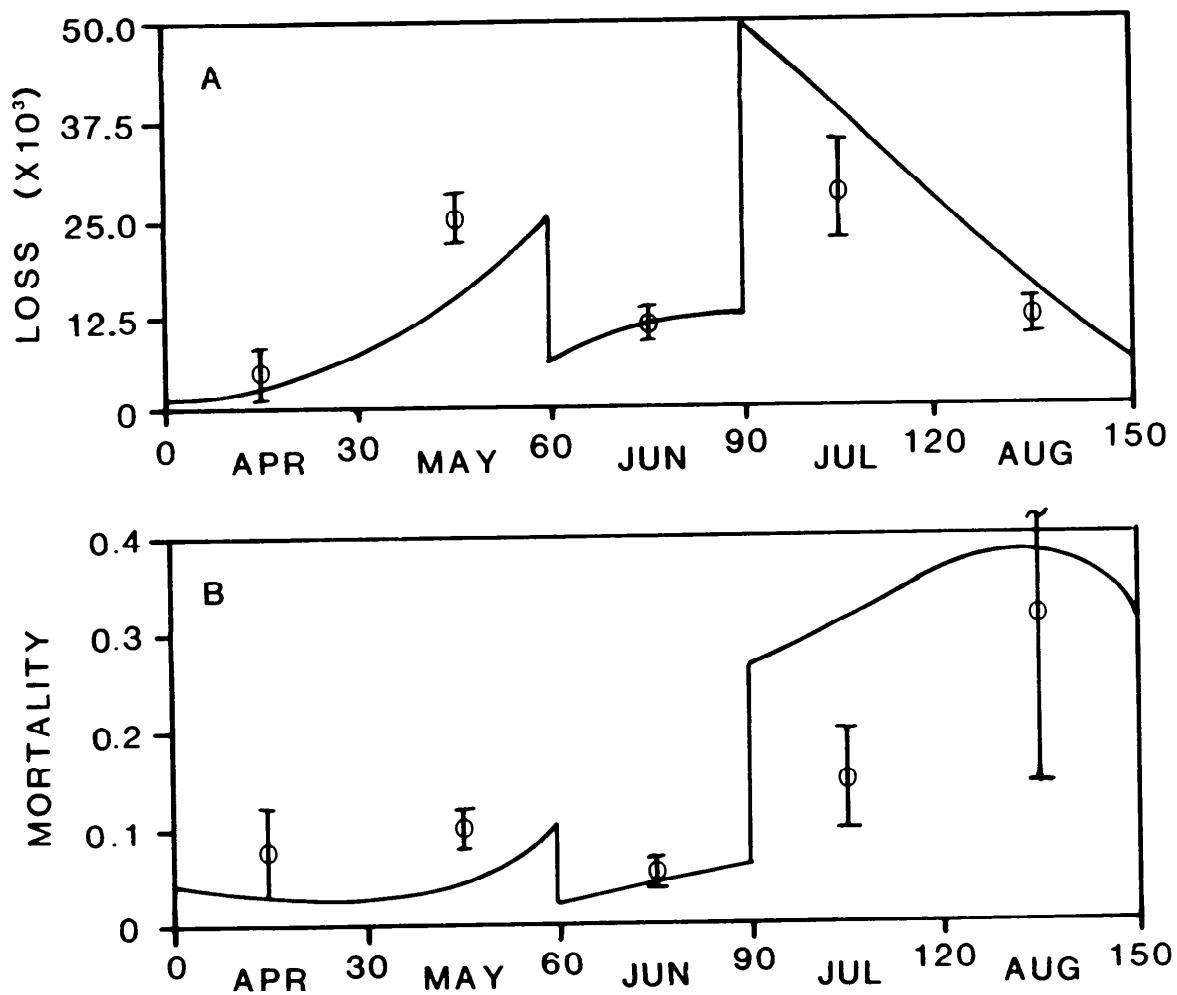


Figure 4. Comparisons of observed (with 95% confidence intervals) and predicted losses (A) and mortality of juvenile salmonids (B) to northern squawfish in John Day Reservoir.

Table 3. Sensitivity analysis showing percentage change in salmonid mortality with changes in input variable or parameter. Variables and parameters are defined in Table 1 and Table 2.

Input	Percent change in input					
	-50	-10	-1	+1	+10	+50
Predators:						
Number (Pn)	-48	-9	-1	1	9	44
Daily mortality (RDm)	1	0	0	0	0	-1
Distribution equation:						
Intercept (p1)	-4	-1	0	0	1	4
Slope (p2)	-3	-1	0	0	1	3
Numerical response (p3)	--	--	--	0	3	18
Active fraction:						
BRZ(RAc1)	-10	-2	0	--	--	--
Reservoir body (RAc2)	-38	-7	-1	--	--	--
Prey:						
Numbers (p6)	31	2	0	0	-2	-3
Day of peak passage (p7)	-11	-4	-1	0	4	22
Days in one SD (p8)	3	1	0	0	-1	0
Residence time (RTm)	-24	-5	0	0	5	28
Residence time-flow equation^a:						
Intercept (p9)	4	1	0	0	-1	-2
Slope (p10)	9	1	0	0	-1	-4
Consumption:						
Maximum rate (RCn _{max})	-49	-10	-4	4	10	43
Intercept:						
BRZ(p14)	10	1	0	0	1	5
Reservoir body (p23)	58	7	1	-1	-6	-23
Response rate:						
BRZ(p15)	-9	-2	0	0	2	11
Reservoir body (p24)	-23	-5	-1	1	5	28
Temperature and discharge:						
Temperature equation:						
Intercept (p21)	-30	-3	0	0	1	-14
Slope (p22)	-44	0	0	0	-7	-15
Peak discharge (p11) ^b	9	1	0	0	1	4
Day of peak discharge (p12) ^b	4	1	0	0	-1	-2
Days in one SD (p13) ^b	9	1	0	0	-1	-2

^a *Alternative to inputting residence time directly.*

^b *only effective when using residence time-flow equation.*

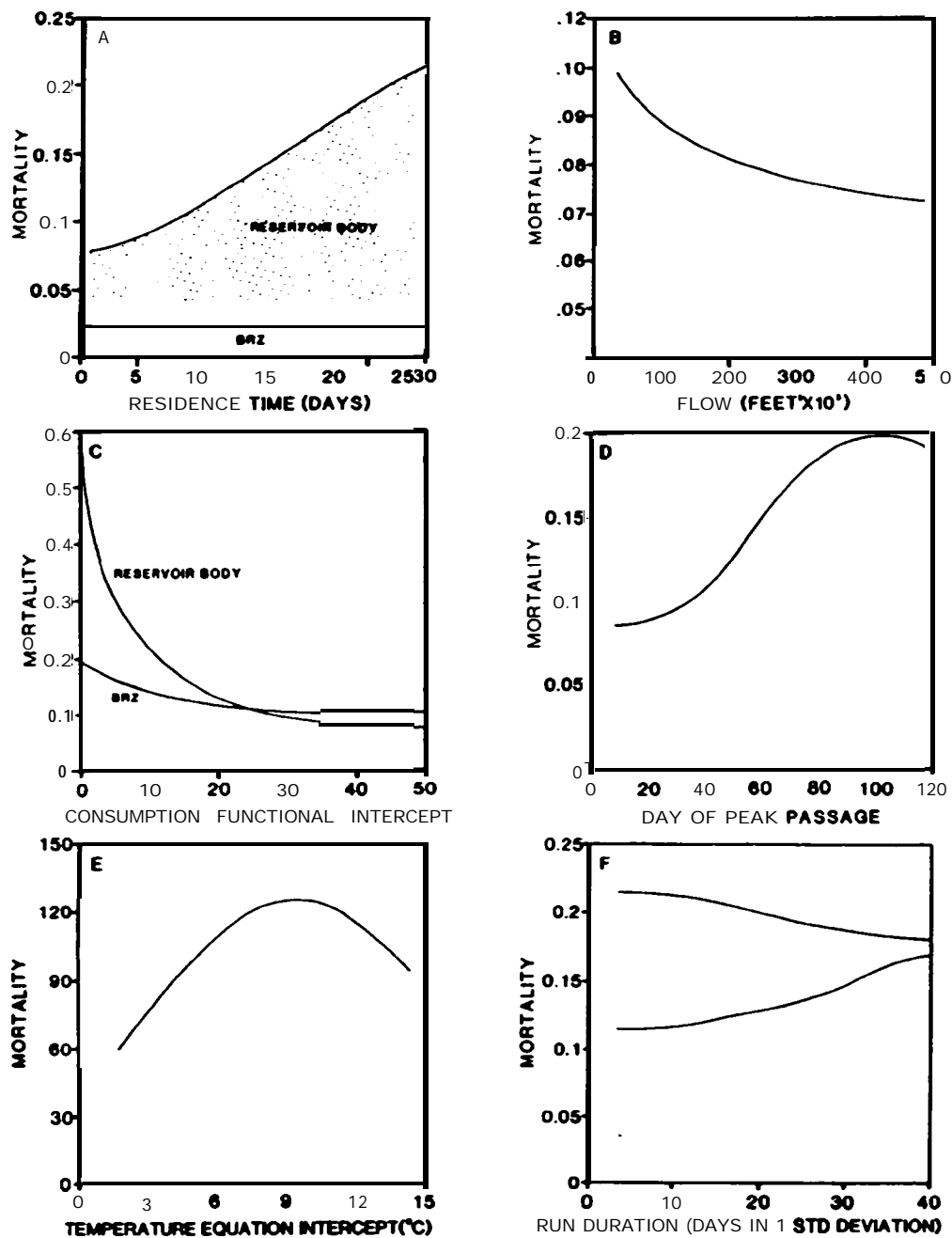


Figure 5. Predicted response in predation mortality to changes in (A) average residence times of juvenile salmonids in John Day Reservoir, (B) flow, (C) the intercept parameter of the functional response equation in the boat-restricted zone and the reservoir body, (D) the timing of juvenile salmonid migration through John Day Reservoir, (E) temperature, and (F) the duration of juvenile salmonids migration through John Day Reservoir.

(Figure 5B). Ye assumed residence time was inversely related to flow. Mortality declined with increasing intercept parameters in the functional response equation for the BRZ and the reservoir (Figure 5C). As the intercept parameter increased, consumption rate declined in both areas. The response in mortality was greater in the body of the reservoir where higher numbers of predators resulted in greater potential for mortality.

Responses of mortality to changes in the timing of peak passage of a single stock and to changes in temperature were dome-shaped. Delay in passage increased mortality until August when high temperature (21°C) caused a reduction in consumption rate (Figure 5D). Reduced mortality of fish entering the reservoir in June during spawning of northern squawfish had little effect on mortality of a single stock because runs were spread over an 80-day period. Increasing the intercept in the temperature equation had the effect of increasing average temperature by the same amount and resulted in a dome-shaped response (Figure 5E). Consumption increased with temperature to the optimum and then declined.

Increases in number of prey produced a complex response in simulated mortality (Figure 6). High mortality at low run sizes (<20 million) resulted from a rapid increase in consumption when passage was low. Declines in mortality at runs of greater than 120 million prey resulted from "swamping" of predators in the reservoir body. "Swamping" refers to increases in passage beyond the physiological capacity (maximum-potential consumption) of predators to consume more prey. Predators in the BRZ were swamped at 50 million, but mortality was little affected because most predation occurred in the reservoir body. This response was similar for early and late runs except the first minima occurred at a lower number in the late run.

The response in mortality to changes in run duration varied with time of year (Figure 5F). Mortality of early run fish increased logistically with increases in the duration of passage (where passage number was constant). During the early run, increases in run duration reduced average daily passage number, and mortality increased because consumption rate on small run sizes was disproportionately high. In contrast, mortality of late run fish declined logistically with an increase in the duration of passage. The day of peak passage of late run fish corresponded to a seasonal peak in mortality driven by temperature, and increasing the duration of the run spread fish into days in which mortality was reduced.

Discussion

Uncertainty analyses confirm that the mortality observed from 1983 through 1986 was similar to that expected over a longer term based on normal annual variation in northern squawfish number, water temperature, and flow. Ye conclude mortality in 1983-86 is representative and we can expect mortality to be a significant fraction of reservoir mortality in most years. However, we do expect some annual variation in predation mortality because our uncertainty

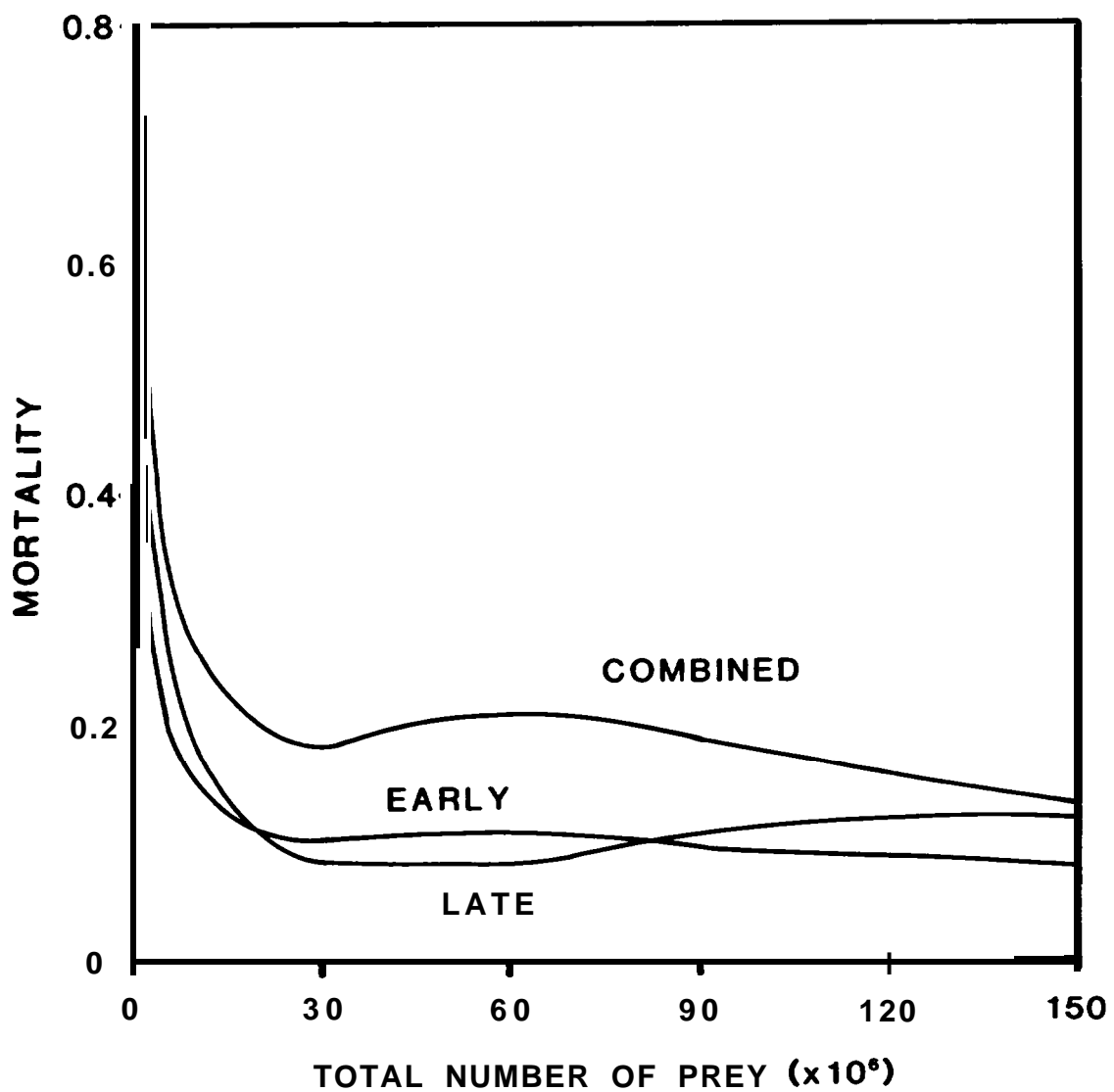


Figure 6. Predicted response in predation mortality to changes in numbers of juvenile salmonids migrating through John Day Reservoir.

analysis predicts a threefold difference between minimum and maximum rates.

This variation is similar to that predicted by Rieman and Beamesderfer (1988) resulting from normal variation in year-class strength of northern squawfish. This implies that variation in year-class accounts for most of the expected fluctuations in mortality through time. This natural variation must be considered when comparing estimates of mortality through time in efforts to evaluate success of management or to identify sources of mortality other than predation.

Sensitivity analyses imply the best avenues for minimizing losses under the assumed set of conditions and relations defined in the model are (1) to reduce predator numbers, (2) to move runs earlier in the year, and (3) to maintain runs no less than current levels. Changes in these factors resulted in relatively large changes in mortality, and all of these factors can be manipulated. Sensitivity analyses also imply actions that reduce predator activity, maximum consumption rates, temperature, and beginning high consumption rate at low prey density could also reduce mortality, but the potential for manipulating these variables seems limited. Mortality will be little affected by changes in predator distribution between the reservoir and BRZ, changes in consumption rate in the BRZ, increases in prey number greater than current levels, and decreases in residence time corresponding to increases in flow.

Reductions in predator number can be expected to cause nearly proportional reductions in mortality if all sizes of predators are equal and numbers or consumption rates of other predators do not increase in response (Rieman and Beamesderfer 1988). Reducing predators appears to be an effective long term strategy (Rieman and Beamesderfer 1988). However, exploitation spread throughout the period of outmigration had relatively little effect within a year because most prey had passed before the number of predators was substantially reduced. Greater benefits would be seen in the following year; hence, removal programs should be geared toward long term benefits.

Any action to pass fish through the reservoir earlier in the year could substantially reduce predation mortality. Fish passing earlier are exposed to predators when low temperature reduces consumption rate. Mortality could be minimized by avoiding dam operations that delay passage, releasing hatchery fish earlier, and enhancing stocks or portions of stocks in which juveniles migrate earlier.

Reductions in the number of salmonids below current levels will drastically increase mortality. Mortality is sensitive to reductions in total run size below 20 million because consumption rate at low run sizes is disproportionately high. Current runs are approximately 20 million salmonids and historical runs were thought to be as large as 4 to 6 times current runs (Northwest Power Planning Council 1986). Increasing the duration of a run has the same effect as decreasing

total number. Both decrease average daily passage during the period of migration. This sensitivity to fewer prey could have important implications for programs aimed at collecting portions of the run and transporting them around sources of mortality (Ebel 1980). Fish remaining in the system will be subjected to increased mortality, which may offset benefits of reduced loss among transported fish. In addition, transportation benefits may be overestimated by comparing survival rates between transported fish and fish left in the river. If transportation substantially reduces the number of fish remaining in the river, mortality among remaining fish will increase well beyond that anticipated for a natural run.

Mortality declines in direct proportion to the proportion of active predators. We are unsure, however, of how activity can be altered. Increased flow might be one avenue. Increased flow in the BRZ forces predators into low velocity refuges (Faler et al. 1988). Some evidence exists for a relationship between flow and inshore distribution in the reservoir body (Beamesderfer and Rieman 1988). Because salmonids typically migrate offshore (telephone interview on 18 December 1988, D. Dauble, Battelle Pacific Northwest Laboratory, Richland, Washington), increased flow may reduce encounters between predators and prey and thus reduce mortality. However, no such relationship between flow and consumption rate has been documented.

Maximum consumption rate is regulated by water temperature, and increased temperature leads to increased mortality except at temperature extremes. The potential for manipulating temperature is unknown. Water temperature is determined by air temperature and the volume of spring runoff but temperature and flow are negatively correlated. Increased flow might be used to reduce water temperature and thereby reduce mortality only if this is a cause-and-effect relationship.

Mortality could be reduced if consumption rate in the reservoir could be manipulated. Mortality was sensitive to changes in intercept and response rate parameters for the functional response equation in the reservoir body. Relative abundance of and preferences for alternative prey might affect these parameters. Switching to alternate prey could reduce rate of increase in consumption (Murdoch and Oaten 1975). The relationship between density of salmonid prey and percentage of salmonids in the diet indicates switching to alternate prey does not occur in the BRZ (Vigg 1988), but switching might be more likely in the reservoir body where prey are more diverse (Poe et al. 1988). Intercept parameters that result in high consumption rates apparently result from preferences for salmonids over other prey (Poe et al. 1988). Increasing alternative prey might reduce or delay switching and reduce mortality as long as increased food does not increase number of predators.

Excluding predators from the BRZ and reducing consumption rate in the BRZ had little effect on total mortality in the reservoir because most predation occurred in the body of the reservoir. Consequently, activities focusing on the BRZ, including changes in dam operations to exclude predators or changes in smolt bypass

locations to reduce consumption rate, will not significantly reduce mortality. In addition, any reduction in predation in the BRZ is offset by a compensatory increase in consumption rate downriver because of the functional response in consumption rate of predators to increases in prey number.

Additional increases in the number of salmonids above current levels would likewise not be expected to substantially reduce mortality. Typical consumption rates of salmonids by northern squawfish are below physiological maximums, and predators throughout the reservoir were not swamped until prey number was 6 times the current level. Substantial reductions in consumption rate were not evident until an even higher number of prey was reached.

Changes in flow are not expected to cause large changes in predation mortality in John Day Reservoir by affecting residence time. Although mortality was sensitive to changes in residence time, residence time was relatively insensitive to changes in flow according to Sims et al. (1984). Decreased flow and increased residence time might increase mortality in reservoirs downstream. If salmonids are delayed throughout the Columbia River, the accumulated delay will result in passage through lower reservoirs when increased temperature causes a much higher rate of consumption.

Our model is an imperfect abstraction subject to uncertainty in estimates of parameters and uncertainty regarding which functions we relate to predation mortality. However, errors in parameter estimates were not important for management-related simulations. Management strategies emerge from the sensitivity to changes in parameters of simulated mortality rather than to estimates of the parameters themselves. The reduction in mortality that resulted from any change depended more on the form of the underlying function than on minor differences in the parameter estimates. Better estimates of parameters would improve the precision of our model predictions, and increased precision would be useful for making management decisions based on quantitative rather than qualitative results. In this case, sensitivity analyses show where additional efforts at parameter estimation would be most effective. We can avoid wasting effort, time and money on unimportant questions by focusing on inputs to which mortality is sensitive.

The precision of the model could be improved with more or better data on the effects of temperature and prey number on consumption in the reservoir. Results were sensitive to these relationships, and relationships were poorly described by existing data. Data on predator distribution between the BRZ and the reservoir, the effect of flow on residence time, and the effect of prey number on consumption in the BRZ were also limited, but little benefit would be gained by collecting more or better data because model results were not sensitive to changes in these inputs.

Sources of uncertainty in forms of functions in the model included assumptions of predator behavior, no differences among prey stocks, and the effects of flow. We assumed that rate of consumption

in the body of the reservoir was a logistic function of the number of prey available, calculated from number entering and residence time. Ye could not verify this assumption. We had no independent estimate of prey density with which to compare consumption rates or predictions of density based on passage and residence time. This assumption was responsible for the dependence of mortality on residence time and flow. Increased residence time increased prey density and mortality.

An alternative assumption would be that predators in the body of the reservoir responded to the number passing rather than to prey density. In this case, a predator would see the same number of prey regardless of how quickly they passed. We assumed that mortality was independent of rate of travel in the BRZ. Thus, the importance of residence time could vary with predator behavior. If predators respond as lie-in-wait predators, reacting only to the number passing, residence time and flow will have no effect on mortality. If predators respond as rover predators, reacting to prey density, residence time will have an effect.

We assumed that early and late runs of salmonids were equivalent. In reality, early runs are mostly steelhead and yearling chinook salmon (Raymond 1988) whereas late runs are primarily subyearling chinook salmon (Miller and Sims 1984). Early-run fish are larger, migrate faster, and are more affected by flow (Miller and Sims 1984; Sims et al. 1984). Differences among stocks may affect rate of predation (Vigg 1988), and these differences may account for some of the unexplained variation in mortality among months.

We were also uncertain of the net effect of flow on predation mortality. Sims and Ossiander (1981) report survival is directly correlated to flow. We identified a mechanism by which flow could affect mortality, but this mechanism does not account for the entire effect. We assumed flow affected residence time, which in turn affected prey density in the reservoir body and consumption rate by predators. However, mortality was relatively insensitive to changes in flow in our model. Our model may underestimate the sensitivity of residence time and hence mortality to changes in flow. Residence time of early-run salmon at low flows may be much greater than Sims et al. (1984) estimated (memorandum dated 14 June 1988, Fish Passage Center, Portland, Oregon).

Flow might affect mortality in ways not included in this model. Flow might alter predator distribution such that encounters between predators and prey are reduced. We discussed how increased flow may force predators inshore where migrating prey are less available. Mortality was sensitive to changes in predator activity, which approximates this change in distribution. Reduced flow might also delay passage such that mortality in downstream reservoirs increases. Delayed migrants pass when increased temperature results in increased consumption rate by predators.

As an alternative explanation we suggest that changes in mortality ascribed to flow are really the result of temperature

differences. Mortality was highly sensitive to changes in temperature. Annual flow and temperature are correlated. Sims and Ossiander (1981) noted mortality was inversely correlated with flow. We hypothesize that mortality is directly affected by temperature. Although flow does have a minor influence on mortality, the relationship suggested by Sims and Ossiander (1981) may be largely the result of covariation with temperature.

Modeling predation mortality has been a valuable exercise despite uncertainties and simplifying assumptions. The model allowed us to organize our understanding of predation in John Day Reservoir and to pull together components of a diverse research effort and present a holistic view of the system. Through this process, critical features of the system and limitations in our understanding were identified. With this understanding we had a systematic means for predicting how the system would respond to changes in components. We could test alternative assumptions of how the systems worked to see if hypothesized effects result. This predictive capability enabled us to ascertain that predation mortality will vary through time and that empirical estimates were representative of the level of predation mortality expected in the long term. We were also able to recommend actions that would reduce mortality and to reject actions that would not achieve desired effects.

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References

- Beauesderfer, R.C. 1988. User's guide for RESPRED: A model of predation by resident fish on juvenile salmonids in a Columbia River reservoir. *In* T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Beauesderfer, R.C., and B.E. Rieman. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: Part III. Abundance and distribution of northern squawfish, walleye, and smallmouth bass. *In* T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86, Final report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.

- Beyer, J.M., G. Lucchetti, and G. Gray. 1988. Gastric evacuation in northern squawfish (*Ptychocheilus oregonensis*). Canadian Journal of Fisheries and Aquatic Sciences 45:548-553.
- Ebel, W. 1977. Major passage problems. Pages 33-39 in E. Schwiebert, editor. Columbia River salmon and steelhead. American Fisheries Society Special Publication 10, Washington D.C.
- Ebel, W.J. 1980. Transportation of chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, smolts on the Columbia River and effects on adult returns. Fishery Bulletin 78:491-505.
- Faler, M., L. Miller, and K. Welke. 1988. Effects of variation in flow on distributions of northern squawfish in the Columbia River below McNary Dam. North American Journal of Fisheries Management 8:30-35.
- Giorgi, A.E., and C.W. Sims. 1987. Estimating daily passage of juvenile salmonids at McNary Dam on the Columbia River. North American Journal of Fisheries Management 7:215-222.
- Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomologist 91:293-320.
- Krebs, C.J. 1985. Ecology: The experimental analysis of distribution and abundance, 3rd edition. Harper and Row, New York.
- Lackey, R.T. 1975. Fisheries and ecological models in fisheries resource management. Pages 241-249 in C.S. Russell, editor. Ecological modeling in a resource management framework. Johns Hopkins University Press, Baltimore, Maryland.
- Miller, D.R., and C.W. Sims. 1984. Effects of flow on migratory behavior and survival of juvenile fall and summer chinook salmon in John Day Reservoir. Report (Contract DE-AI79-83BP39645) to Bonneville Power Administration, Portland, Oregon.
- Murdoch, W.W., and A. Oaten. 1975. Predation and population stability. Advances in Ecological Research 9:1-131.
- Northwest Power Planning Council. 1986. Compilation of information on salmon and steelhead losses in the Columbia River Basin. Unpublished report. Portland, Oregon.
- Overton, W.S. 1977. A strategy of model building. Pages 49-74 in C.A.S. Hall, editor. Ecosystem modeling in theory and practice: An introduction with case histories. Wiley and Sons, New York.

- Peterman, R.M., and M. Gatto. 1978. Estimation of functional responses of predators on juvenile salmon. *Journal of the Fisheries Research Board of Canada* 35:797-808.
- Poe, T.P., H.C. Hansel, S. Vigg, D.E. Palmer, and L.A. Pendergast. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: Part I. Feeding ecology of northern squawfish, walleye, smallmouth bass, and channel catfish during the juvenile salmonid out-migration. *In* T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Raymond, H.L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. *Transactions of the American Fisheries Society* 108:505-529.
- Raymond, H.L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook and steelhead in the Columbia River Basin. *North American Journal of Fisheries Management* 8:1-24.
- Rieman, B.E., and R.C. Beamesderfer. 1988. Population dynamics of northern squawfish and potential predation on juvenile salmonids in a Columbia River reservoir. *In* T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Rieman, B.E., R.C. Beamesderfer, and S. Vigg. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River reservoir: Part IV. Total loss and mortality of juvenile salmonids to northern squawfish, walleye, and smallmouth bass. *In* T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Sims, C.W., R.C. Johnsen, and D.A. Brege. 1982. Migrational characteristics of juvenile salmon and steelhead trout in the Columbia River system, 1981. Report (Contracts DACW68-78-C-0051 and DACW57-83-F-0314) to U.S. Army Corps of Engineers, North Pacific Division, Portland, Oregon.
- Sims, C.W., A.E. Giorgi, R.C. Johnsen, and D.A. Brege. 1984. Migrational characteristics of juvenile salmon and steelhead in the Columbia River basin, 1983. Report (Contracts DACW68-78-C-0051 and DACW57-83-F-0314) to U.S. Army Corps of Engineers, North Pacific Division, Portland, Oregon.

- Sims, C.W., and F.J. Ossiander. 1981. Migrations of juvenile chinook salmon and steelhead in the Snake River, from 1973 to 1979, a research summary. Report (Contract DACW68-78-C-0038) to U.S. Army Corps of Engineers, North Pacific Division, Portland, Oregon.
- U.S. Army Corps of Engineers. 1957,1958,....,1986. Annual fish passage report, Columbia and Snake Rivers, for salmon, steelhead, and shad. North Pacific Division, Portland, Oregon.
- Vigg, S. 1988. Functional response of northern squawfish predation to salmonid prey density in McNary tailrace, Columbia River. In T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Vigg, S., and C.C. Burley. 1988. Maximum consumption rates of northern squawfish in John Day Reservoir, Columbia River. In T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.
- Vigg, S., T.P. Poe, L.A. Prendergast, and H.C. Hansel. 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir: Part II. Consumption rates, diel feeding chronology, and daily rations of northern squawfish, walleye, smallmouth bass, and channel catfish. In T.P. Poe and B.E. Rieman, editors. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final report (Contracts DE-AI79-82BP34796 and DE-AI79-82BP35097) to Bonneville Power Administration, Portland, Oregon.